

Phytoplankton Community Structure and Primary Productivity
in Two Florida Lakes

By

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Abstract of Dissertation Presented to the Graduate Council
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PHYTOPLANKTON COMMUNITY STRUCTURE AND PRIMARY PRODUCTIVITY
IN TWO FLORIDA LAKES

By

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The relationships between primary productivity and algal species assemblages, succession and diversity were examined. Primary productivity was determined using the ^{14}C technique. In an oligotrophic lake, a bimodal pattern of primary productivity coincided with the appearance of diatoms, and blooms were followed by increases in the low-phosphate-tolerant genus Dinobryon. Nannoplankton were found to dominate primary productivity in spring and winter in the surface waters, and throughout the year at 1.5 meters. In a eutrophic lake, a persistent summer bloom of heat-tolerant blue-green algae was superimposed on the bimodal pattern of spring and autumn blooms. Nannoplankton were found to be of importance only in the spring bloom. No correlation between algal diversity or algal numbers and primary productivity was found in either lake. Primary productivity was significantly correlated with chlorophyll "a" concentrations in the surface waters of the oligotrophic lake.

INTRODUCTION

Primary productivity and related aspects of plankton community structure have long been subjects of limnological interest, but most research has resulted in purely descriptive data for specific bodies of water. With the use of laboratory and field data from long-term studies, attempts have recently been made to integrate these descriptive data in order to explain the relationships between primary productivity and phytoplankton composition, diversity and succession. Margalef (1960) emphasized the importance of this approach in opening new avenues of investigation and analysis.

Studies of algal succession in lakes over long periods of time have led to the formulation of hypotheses about the species or species groups expected under certain biological and chemical conditions (Margalef, 1958, Olive et al., 1969). The physical, chemical and biological causes of succession have been directly correlated with the requirements of several species groups (Round, 1958, Brook, 1965, Hutchinson, 1967, Holland, 1968) and have resulted in the recognition of certain indicator species for various water types.

The direct relationships between a particular algal species or species assemblage and primary productivity have been determined by use of tracer studies (Olive et al., 1968), studies of diversity (Patten, 1963, Margalef, 1965, Richerson et al., 1970) and chlorophyll content (Parsons and Strickland, 1963, Lorenzen, 1970), and direct observation. One result of the integration of these data has been

the discovery of the relatively large contribution of nanoplankton (those algae and bacteria that are not retained by a #25 mesh plankton net) to primary productivity in lakes. Rodhe (1955), Pavoni (1963), Lund (1964) and Anderson (1965) indicated that nanoplankters are often numerically dominant, even when not dominant in biomass. Rodhe (1962) attributed the importance of the nanoplankton to the possibility of their utilization of organic material in the water and to their apparent tolerance of low light conditions. These conditions would allow nanoplankton to survive and reproduce when larger phytoplankters could not. The numerical dominance results in the establishment of an important food source for zooplankton (Rodhe, 1955, Lindeman, 1942, Gliwicz, 1968, 1969a, 1969b, 1969c).

Rodhe et al. (1960) showed that nanoplankton may dominate primary productivity even when they lack numerical dominance. Fogg (1965), Findenegg (1965) and Olive et al. (1968) stated that nanoplankton assimilation of carbon is greater than that of larger algal cells due to the larger surface-to-volume ratio of the smaller cells. The nanoplankton dominance of primary productivity varies with the trophic state of the lake, the time of year and depth of the lake. Nanoplankton contribute the major portion of primary productivity in oligotrophic lakes in winter and spring at all depths, and throughout the year in deeper waters (Goldman, 1961, Goldman and Wetzel, 1963, Pavoni, 1963, Eberly, 1964, Geen and Hargrave, 1966, Gliwicz, 1967 and Frey, 1969).

This study was undertaken to determine the relationship between the phytoplankton community structure and primary productivity, with particular emphasis on the relative contributions of different size groupings. Two semi-tropical Florida lakes at either end of the

oligotrophic-eutrophic continuum were selected in order to present clear-cut comparisons between lakes of different trophic states. Determinations of productivity, chlorophyll concentration, algal composition, succession and diversity, and zooplankton composition were made for each size grouping.

THE STUDY AREA

Lake McCloud, an oligotrophic sand-hill lake located 40 kilometers (25 miles) east of Gainesville, Florida, has a surface area of roughly 8 hectares and an average depth of 5 to 7 meters. The lake thermally stratifies only rarely in summer, and light penetrates to a depth of about 3.3 meters. Chemical characteristics of Lake McCloud may be seen in Table 1. Other studies on various aspects of the chemistry and biology of Lake McCloud may be found in Colson (1969), Maslin (1969), Maslin (1970) and Brezonik et al. (1969).

Biven's Arm is a shallow eutrophic lake south of Gainesville, and has a surface area of 60 hectares and an average depth of 1.5 meters (Nordlie, 1967). The lake never thermally stratifies, and light penetration is limited year-round by dense algal blooms. Chemical parameters are outlined in Table 1. Detailed studies of the chemistry and biology of Biven's Arm may be found in Nordlie (1967).

TABLE 1

Chemical characteristics of the study areas

Constituent	Lake McCloud	Biven's Arm
pH*	5.2 - 7.9	7.8 - 9.8
acidity, ppm CaCO_3	3.5	2.0 - 4.0
alkalinity, ppm*	3.0	99.3 - 176.0
dissolved organic PO_4 , mg PO_4/l	0.012	0.72 - 1.84
nitrate, mg NO_3/l	0.041	0.0 - 0.3

* from this study (1970-1971);
all other Lake McCloud data from
Brezonik et al. (1969), and all
other Biven's Arm data from
Nordlie (1967).

METHODS AND MATERIALS

Sampling occurred at two-week intervals from February, 1970, through February, 1971. Surface samples were collected directly by immersion of a five-gallon plastic carboy, while samples from deeper levels were collected with a Van Dorn sampler and transferred to a carboy. The water was then returned to the laboratory for analysis and treatment.

Algal size groups were separated by filtering the lake water through bolting cloth of three mesh sizes. Each sample was divided into four groups - unfiltered, less than $158\ \mu$ (#10 silk), less than $76\ \mu$ (#20 silk), and less than $70\ \mu$ (#25 silk). The latter group, for purposes of this study, has been designated as nanoplankton, in accordance with those definitions reported by Dussart (1965), and Williams and Murdoch (1966). Filtered and unfiltered water was then placed in BOD bottles for further processing.

Primary productivity was determined by the ^{14}C Carbon method as described by Strickland and Parsons (1968), modified for fresh water as suggested by Arthur and Rigler (1967) and for liquid scintillation counting as reported by Lind and Campbell (1969). Light and dark bottle pairs were inoculated with $2.5\ \mu\text{Curies}$ of $\text{Na}^{14}\text{CO}_3$. Samples were incubated for 4 to 8 hours in a shaker at 20°C and a light range of 500 to 700 lux rather than at varying conditions, or in situ, to facilitate comparison of the two lakes. Fifty-milliliter

aliquots of each size sample were fixed with 40 percent formaldehyde, filtered through 0.8 μ millipore filters at low pressure, dried over silica gel for a minimum of 24 hours, and counted in a liquid scintillation counter. Some samples were filtered through 0.47 μ millipore filters, and samples of filtered water from both size filters were counted. No apparent difference was noted between the two size filters, with each size filtering out all algae found in the samples. Equal portions of the unfiltered size grouping were further subdivided by filtration through 5 μ and 8 μ millipore filters.

Carbon fixed as $\text{mg C/m}^3 \text{ hr}$ was determined from the formula:

$$\frac{(R_1 - R_d) \times W \times 1.05 \times 1000 \text{ l/m}^3}{h \times A}$$

where:

R_1 = counts per minute (cpm) in the light bottle,

R_d = cpm in the dark bottle,

W = weight in mg/l of carbonate present in water,

h = incubation time in hours, and

A = activity added in cpm.

The figure 1.05 is a factor that adjusts for possible isotope effects caused by the difference in size between ^{12}C and ^{14}C .

A replicate BOD bottle for each size group was analyzed prior to incubation for water temperature, pH and alkalinity (Standard Methods, 1960). These three factors were used to determine the amount of carbonate in the sample according to the method outlined by Saunders, Trama and Bachmann (1962). Portions were also preserved with 40 percent formaldehyde and set aside for the counting, identification and measurement of phyto- and zooplankton. Identification to genus was made when possible for algae, and to class for zooplankton (Prescott, 1954, Edmondson, 1966).

Additional aliquots were filtered through millipore filters for collection of and analysis of chlorophyll according to the methods outlined by Richards (1952), Richards and Thompson (1952) and Creitz and Richards (1955), and as modified by Parsons and Strickland (1963). Size groups were the same as those established by filtration for primary productivity. An additional replicate BOD bottle was incubated with the radioactive samples, and analyzed for chlorophyll, algae and zooplankton in a similar manner after incubation.

Statistical analyses of correlation were used as described in Snedecor and Cochran (1967). Calculations were made with the aid of programs for the Olivetti Programma 101 and the Monroe Epic calculators.

RESULTS

Primary Productivity

Primary productivity (mg carbon fixed/m³ hr) of unfiltered samples from surface waters is shown in Figure 1, and that of nanoplankton samples from surface waters is shown in Figure 2. In Lake McCloud, peaks in productivity occurred in May-June, 1970, and in October-November, 1970. At these times, productivity of Lake McCloud exceeded that of Biven's Arm even though Biven's Arm had a persistent algal bloom throughout the year. Similar trends in all data were exhibited for all size groups and are shown in the Appendix (Tables A1 - A6).

Productivity for deeper waters in Biven's Arm was measured in March, September and December, 1970, and in February, 1971. Due to the shallow nature of the lake, wind mixing of the waters and low light penetration due to algal blooms, the euphotic zone was limited to one meter or less. Samples were taken at half the depth of the euphotic zone (0.3 m), and no differences in trends from surface were noted in these samples. Table 2 shows that productivity at 0.3 m exceeded that of the surface with the exception of the December, 1970, sample.

Primary productivity at 1.5 m below the surface in Lake McCloud was measured at more frequent intervals than at the 0.3 m depth in Biven's Arm. The depth of 1.5 m was selected as being half the depth of the euphotic zone in order to compare data with those taken from Biven's Arm. Productivity for the unfiltered and nanoplankton

TABLE 2

Primary productivity* at two depths in Biven's Arm

Date	Surface		0.3 m	
	unfilt.	nanno.	unfilt.	nanno.
March 17, 1970	1.44	0.00	4.40	4.07
September 24, 1970	6.49	3.96	7.73	5.90
December 6, 1970	1.37	1.01	0.33	0.72
February 19, 1971	1.78	1.78	4.19	2.35

* in mg C fixed/m³ hr

Figure 1. Variations in primary productivity for unfiltered fractions from surface waters in Lake McCloud and Biven's Arm, 1970-1971. Data points are connected to indicate general trends and are not meant to imply anything about the productivity continuum.

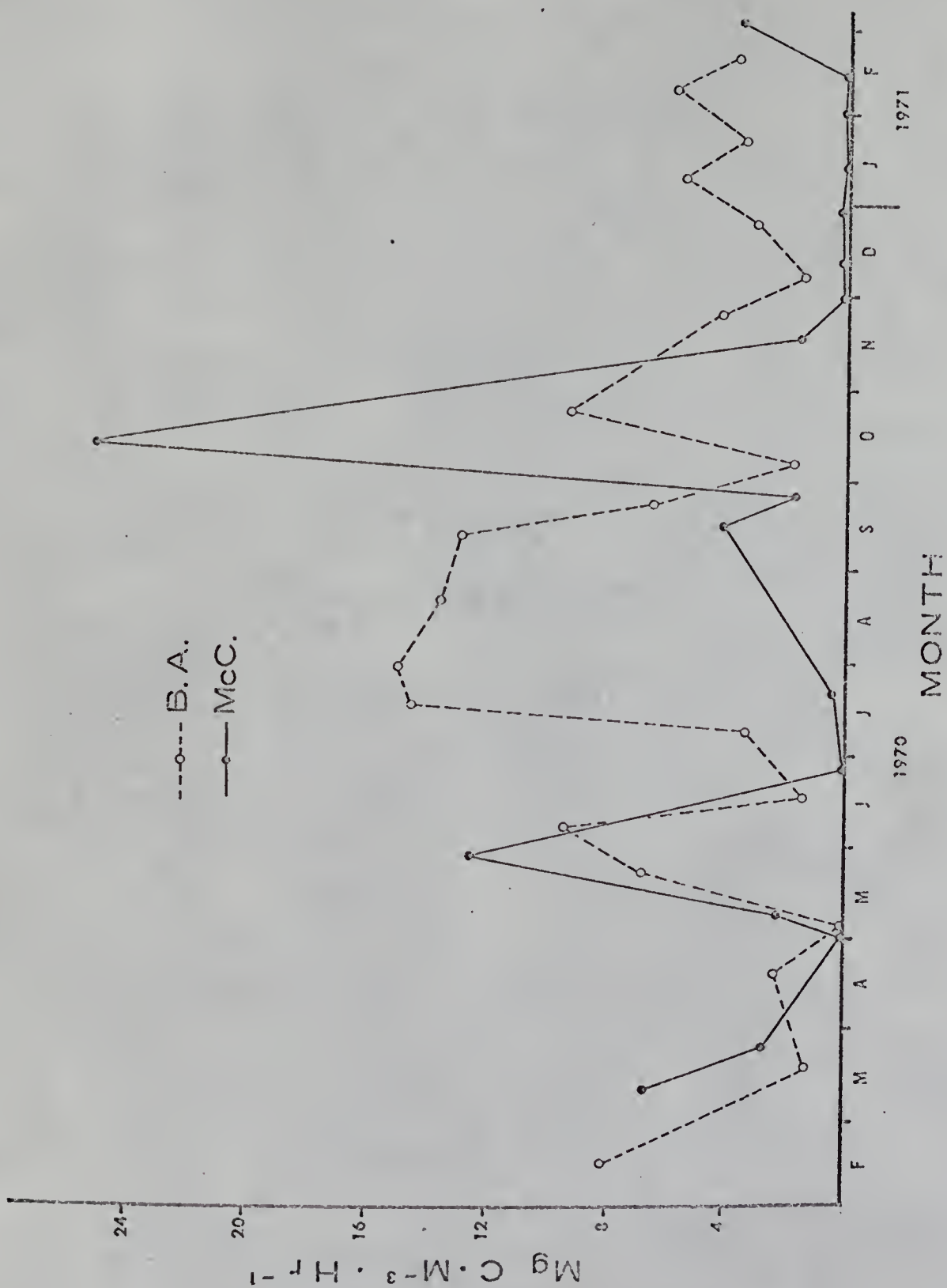
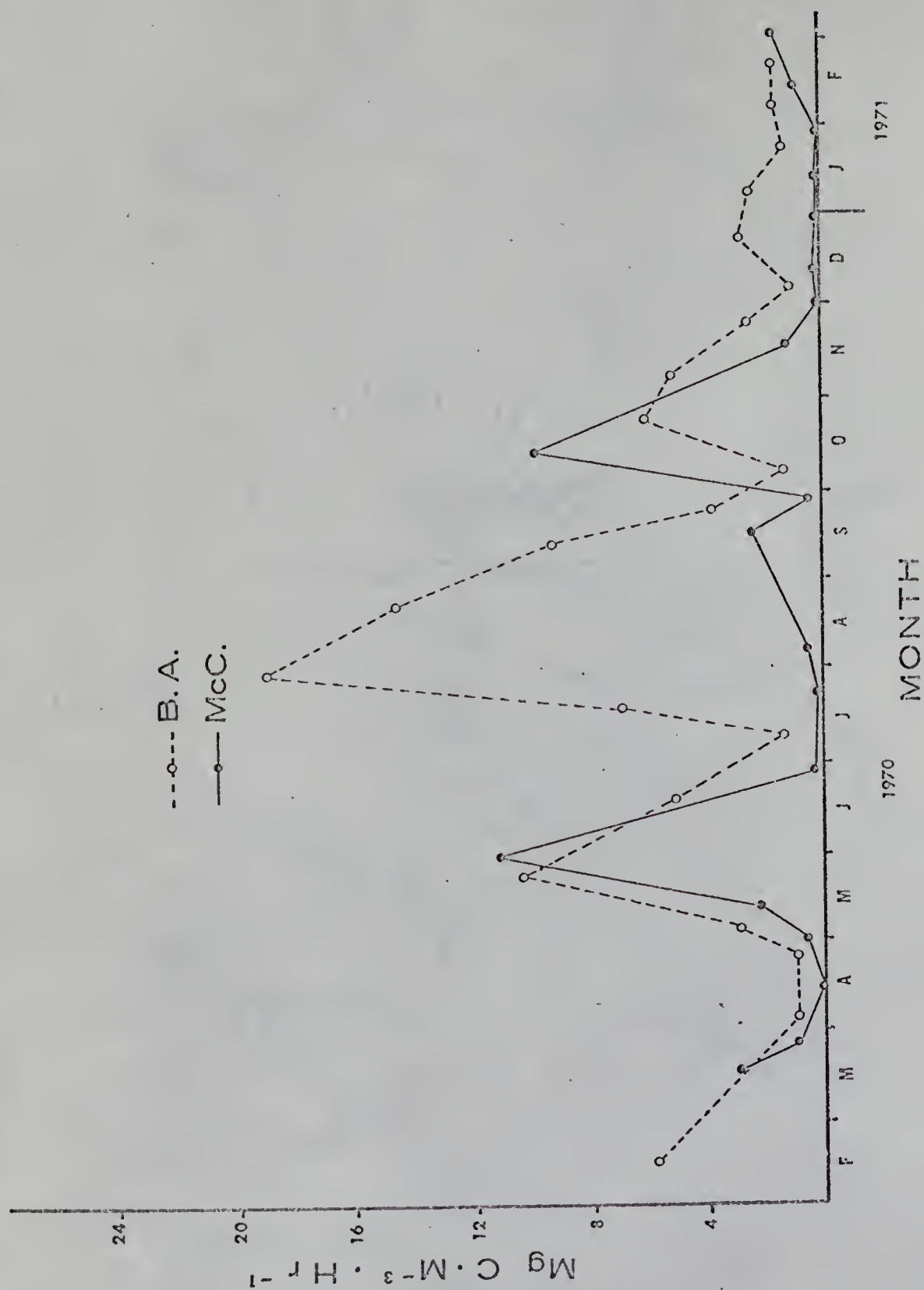


Figure 2. Variations in primary productivity for nanoplankton fractions from surface waters in Lake McCloud and Biven's Arm, 1970-1971. Data points are connected to indicate general trends and are not meant to imply anything about the productivity continuum.



samples from 1.5 m are shown in Figure 3; and Tables A7 through A-10 show these values for the other size groupings. Trends are similar to those shown in Figures 1 and 2, although the magnitude of productivity and the fluctuations were less in the deeper water.

Ratios of the productivity of the nanoplankton fraction to the productivity of the unfiltered fraction are shown in Figures 4 and 5. The ratios often exceed 1.0, and this phenomenon has been attributed by Gliwicz (1967) to the reduction of inter- and intraspecific competition. Filtration results in the removal of algae and a subsequent increase in available nutrients, light and space for the remaining cells. In addition, the reduction in numbers of algae could result in the reduction of possible inhibitive activities of some species, and filtration reduces grazing pressure by the removal of zooplankton. The ratios for Lake McCloud exceed those of Biven's Arm in April-May, 1970, and in October, 1970 - March, 1971. The ratios for deeper waters in Lake McCloud exceed those for surface waters for the same lake from June, 1970, through November, 1970.

Chlorophyll

Total chlorophyll in mg/ml in unfiltered and nanoplankton fractions is shown in Figures 6 and 7 respectively. In Biven's Arm, chlorophyll content roughly corresponds with the curve for primary productivity, with peaks in chlorophyll concentration appearing to lag behind productivity as much as two weeks. Total chlorophyll concentrations in Lake McCloud appear to be much more stable. Primary productivity showed no correlation with total chlorophyll or with chlorophyll "a" with the exception of a positive correlation between productivity and chlorophyll "a" in surface waters in Lake McCloud (Table 3).

Figure 3. Variations in primary productivity for unfiltered and nanoplankton fractions from 1.5 m in Lake McCloud, 1970-1971. Data points are connected to indicate general trends and are not meant to imply anything about the productivity continuum.

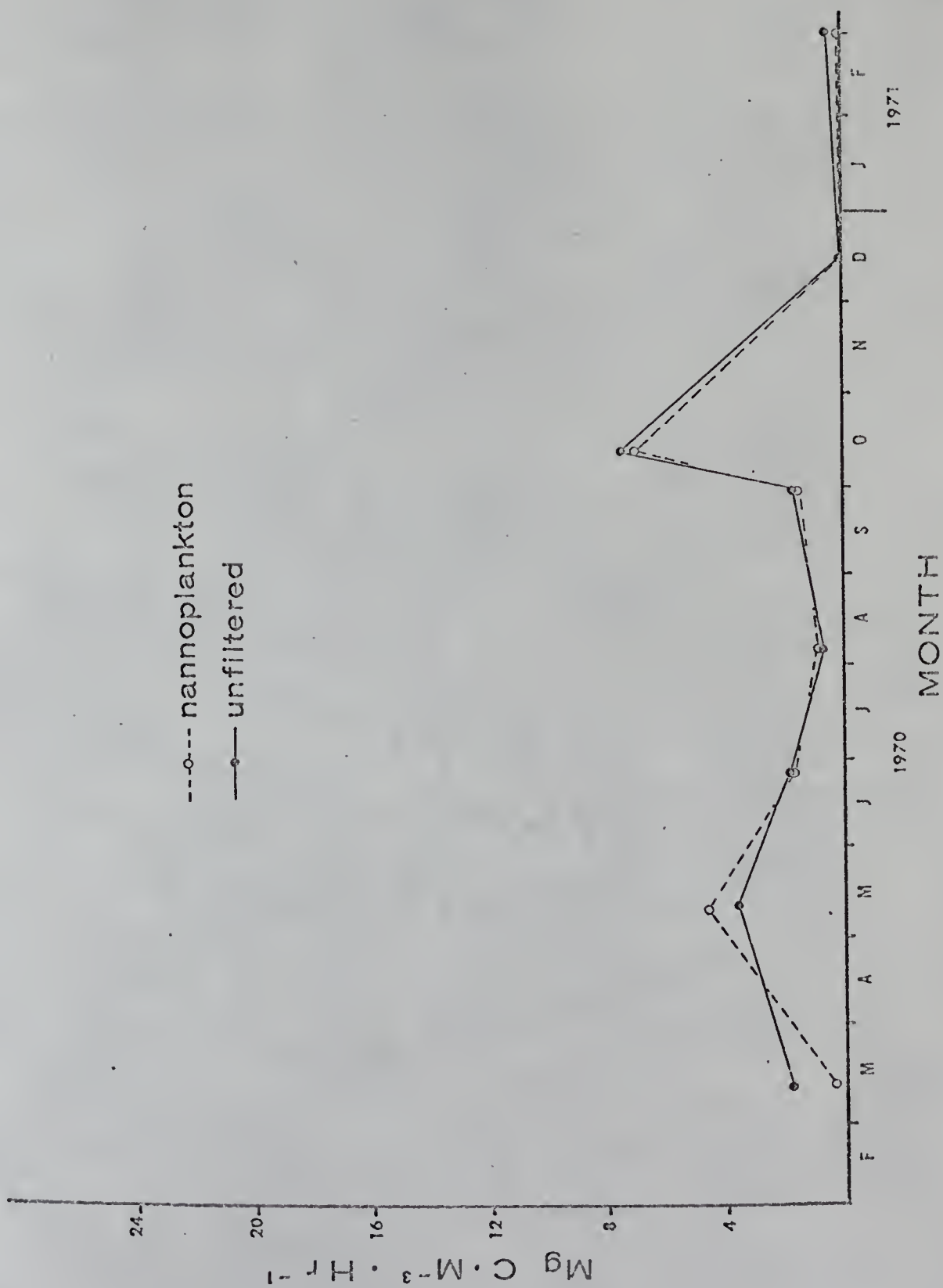


Figure 4. Variations in the ratio of primary productivity of nanoplankton fractions to primary productivity of unfiltered fractions from surface waters in Lake McCloud and Biven's Arm, 1970-1971.

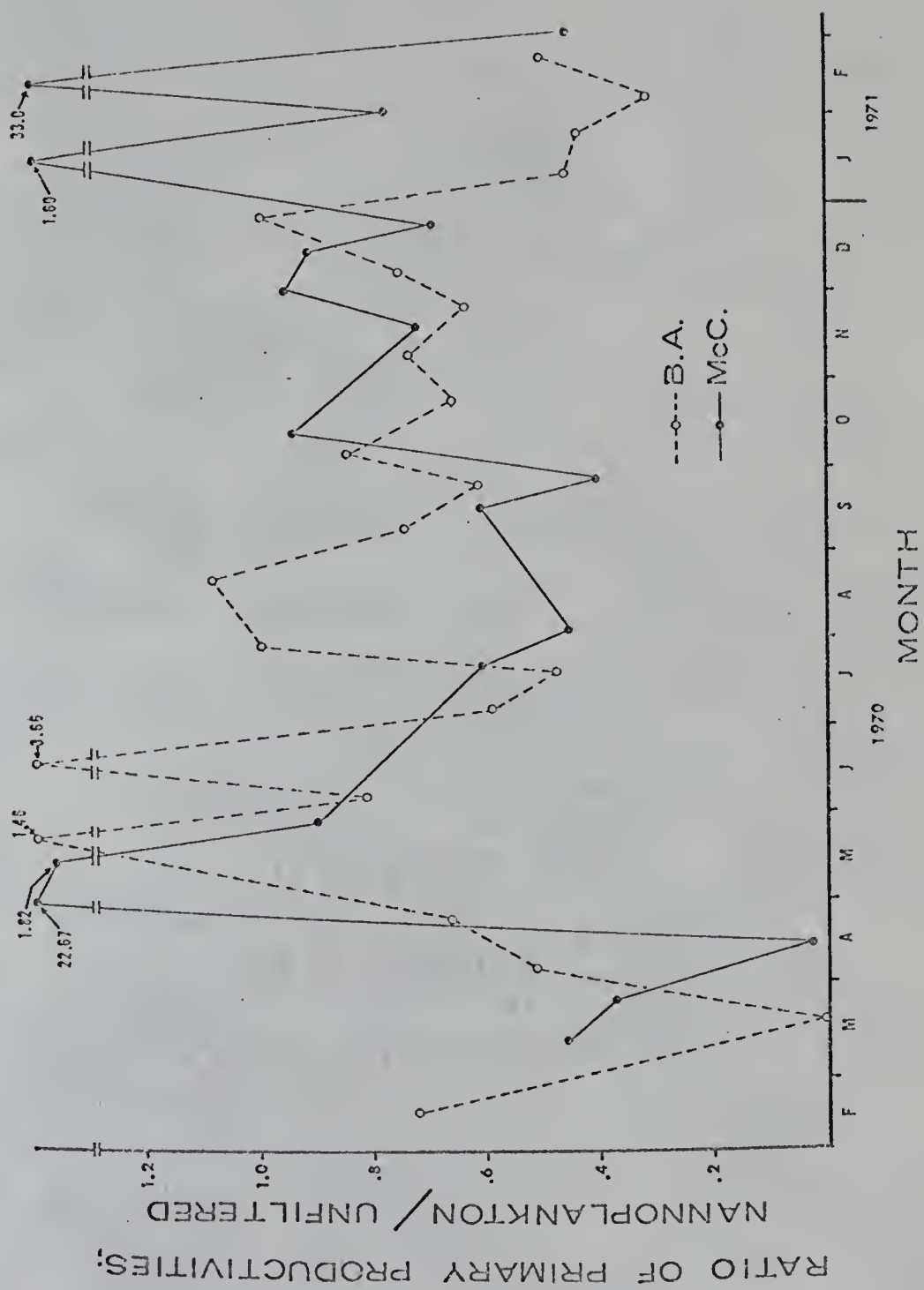


Figure 5. Variations in the ratio of primary productivity of nanoplankton fractions to primary productivity of unfiltered fractions from surface waters and 1.5 m in Lake McCloud, 1970-1971.

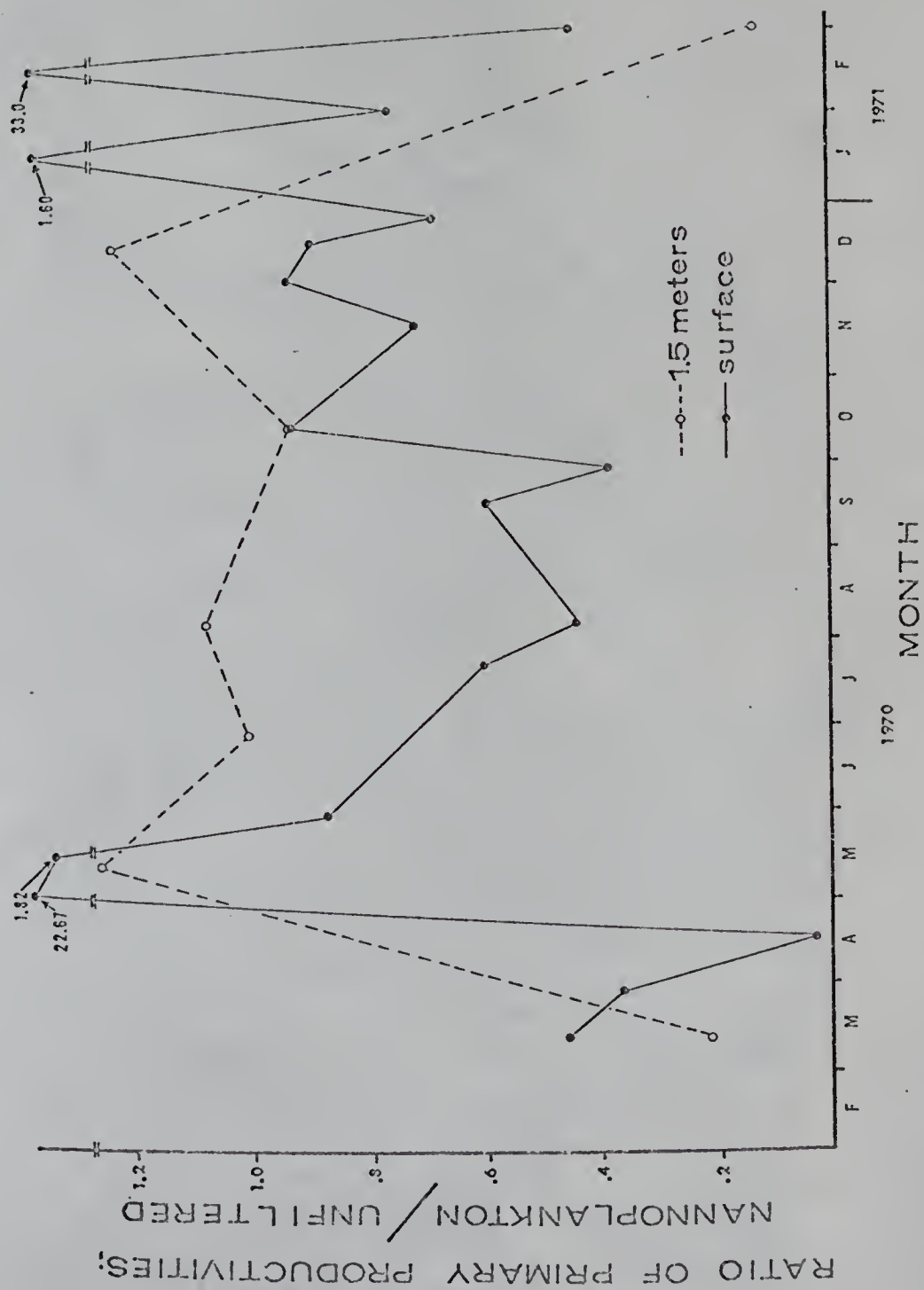


Figure 6. Variations in total chlorophyll concentration in unfiltered samples from surface waters in Lake McCloud and Biven's Arm, 1970-1971.

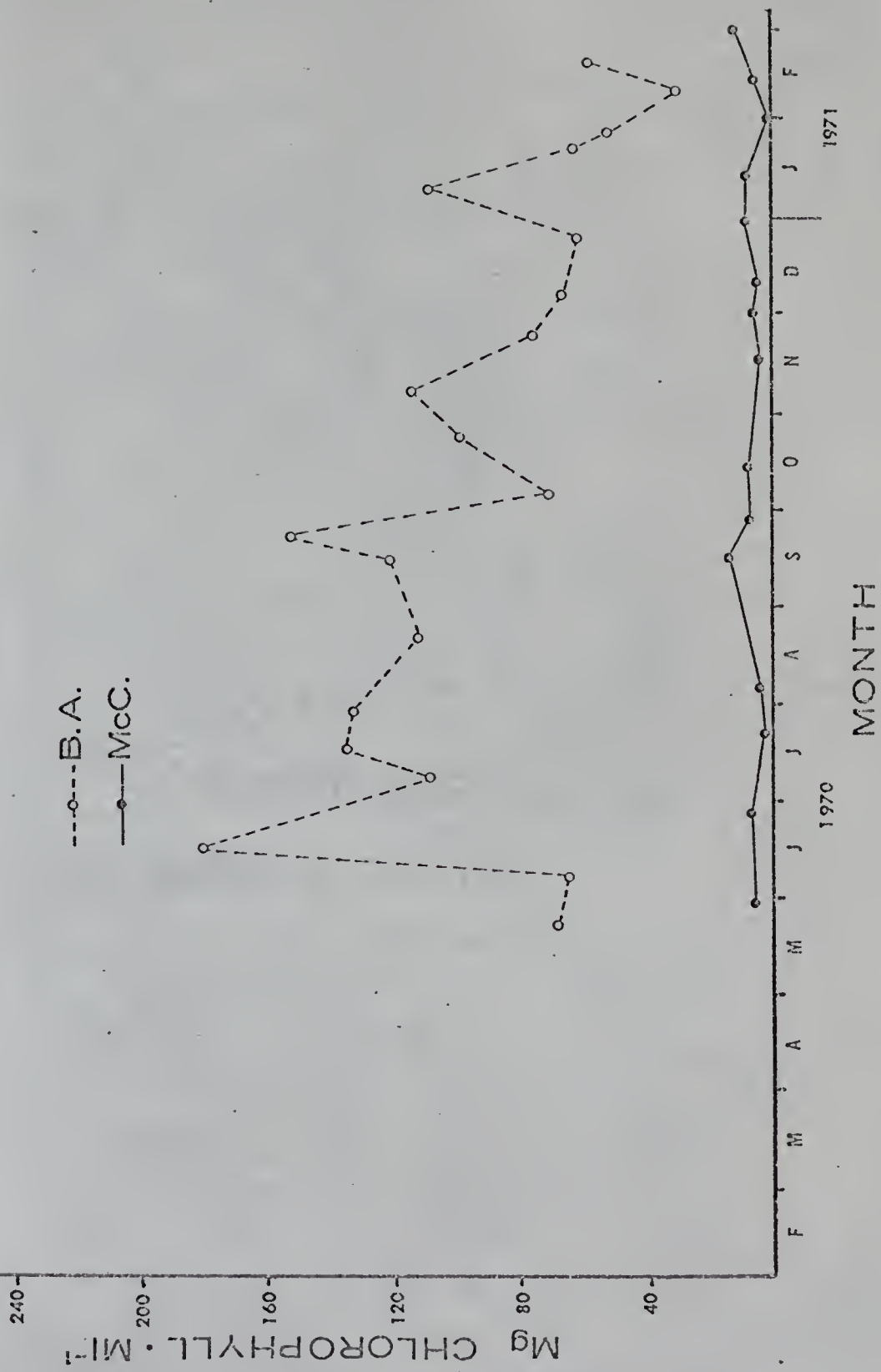


Figure 7. Variations in total chlorophyll concentration in
nannoplankton samples from surface waters in
Lake McCloud and Biven's Arm, 1970-1971.

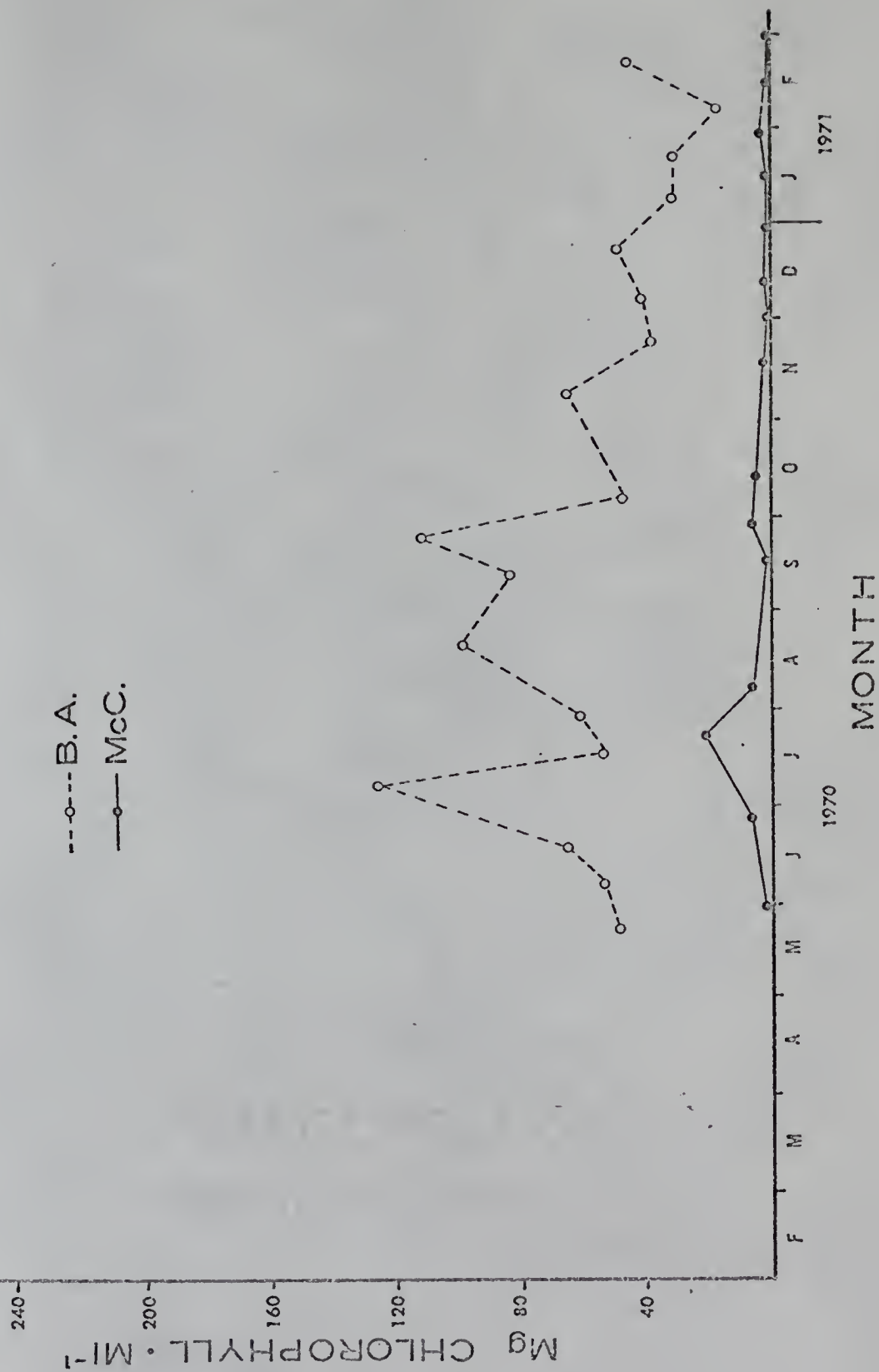


TABLE 3

Relationships between chlorophyll and primary productivity

Lake-depth	Chlorophyll "a"		Total Chlorophyll	
	r	95% bounds on ρ	r	95% bounds on ρ
Biven's Arm - surf.	0.28	$-.216 \leq \rho \leq .664$	0.11	$-.380 \leq \rho \leq .551$
McCloud - surf.	0.55*	$-.020 \leq \rho \leq .804$	0.28	$-.281 \leq \rho \leq .706$
McCloud - 1.5 m	0.58	$-.438 \leq \rho \leq .947$	0.59	$-.422 \leq \rho \leq .948$

* significant at .05 level

Chlorophylls "a" and "c" were the major types present in both lakes throughout the year. These types are indicative of the presence of diatoms, dinoflagellates or blue-green algae (Delevoryas, 1966, Hutchinson, 1967).

Chlorophyll concentrations from incubated samples showed some differences in content from those measured prior to incubation, such as those variations reported by Geen and Hargrave (1966). In some cases, chlorophyll content increased during incubation while in others, chlorophyll concentration decreased. No consistent trend for loss or gain was noted for any size group in either lake, nor could losses or gains be correlated with changes in phyto- or zooplankton numbers. These variations were possibly due to random variability in chlorophyll in natural populations as noted by Yentsch and Ryther (1957) rather than to the influence of the process of incubation.

Species Composition

It became evident during examination of samples that certain algae, commonly occurring in multicellular colonies, had cells that were either too small or too numerous to count. Each colony was therefore counted as a "unit" equivalent to a cell of a solitary species. Figures 8 and 9 show the percent of the total algal count for the algae found in the two lakes. Total unit counts (Tables A1 - A10) and species (Table A12) were similar for both depths in each lake. In nanoplankton samples, species were similar to those found in unfiltered samples in both lakes. This latter phenomenon was reported by Pavoni (1963).

Algal assemblages show a dominant blue-green algal bloom (Anabaena sp., Microcystis aeruginosa) in the summer months in

Biven's Arm, and a winter and spring assemblage of diatoms (Melosira granulata) and small colonial green algae (Pediastrum spp., Sphaerocystis sp., Scenedesmus spp.). In Lake McCloud, algal species were predominantly small dinoflagellates, chrysophytes (Dinobryon sertularia, Mallomonas sp.), and desmids (Staurostrum spp.). Total numbers of algal units did not correlate with primary productivity (Table 4) and did not change with respect to numbers or species composition during incubation.

Algal diversity (Figure 10) for unfiltered waters was calculated using the Shannon index of diversity (Hutchinson, 1967):






$$D = - \sum_{i=1}^n p_i (\log_2 p_i)$$

where p_i is the probability of occurrence of the i th species, i going from 1 to n . Diversity showed no correlation with primary productivity (Table 5). Diversity remained relatively constant throughout the year in Lake McCloud while it decreased in the summer in Biven's Arm.

Zooplankton composition in percent of total count for each lake is shown in Figures 11 and 12. Biven's Arm was dominated by small rotifers and a colonial ciliate while a shelled amoeba was the dominant species in Lake McCloud. Peaks in numbers of zooplankton occurred in June, September and December, 1970, in Biven's Arm, and in July and October, 1970, in Lake McCloud as well as January, 1971 (Table A11). Comparisons between algal diversity and zooplankton showed no correlation (Table 6). Numbers of zooplankton were similar at the surface and at 1.5 m in Lake McCloud.

Figure 8. Seasonal fluctuations in phytoplankton in Biven's Arm, 1970-1971. (Depth of pattern represents the percent of the total phytoplankton comprised by each group. For example, note that during the month of July, 1970, Microcystis aeruginosa increased from 37% to 71% of the phytoplankton, while Anabaena sp. decreased from 63% to 29% of the phytoplankton.)

Key:

	<u>Microcystis aeruginosa</u>		<u>Anabaena</u> sp.
	<u>Melosira granulata</u>		other diatoms
	green algae (including desmids)		

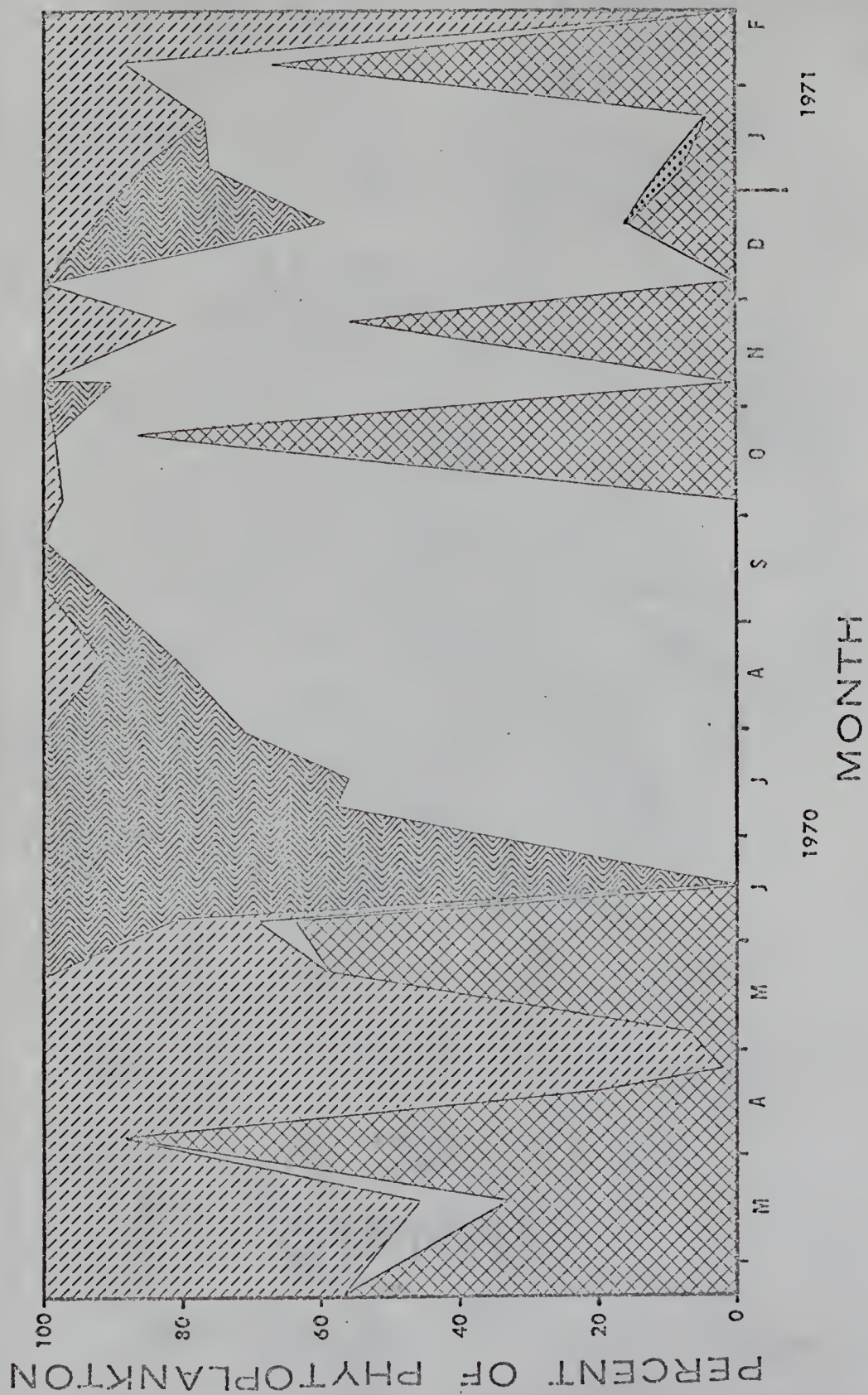


Figure 9. Seasonal fluctuations in phytoplankton in Lake McCloud, 1970-1971.
 (Depth of pattern represents the percent of total phytoplankton
 comprised by each group. Read in the same manner as Figure 8.)

Key:

	<u>Dinobryon sertularia</u>		filamentous green algae
	dinoflagellates		diatoms
	green algae		<u>Mallomonas</u> sp.

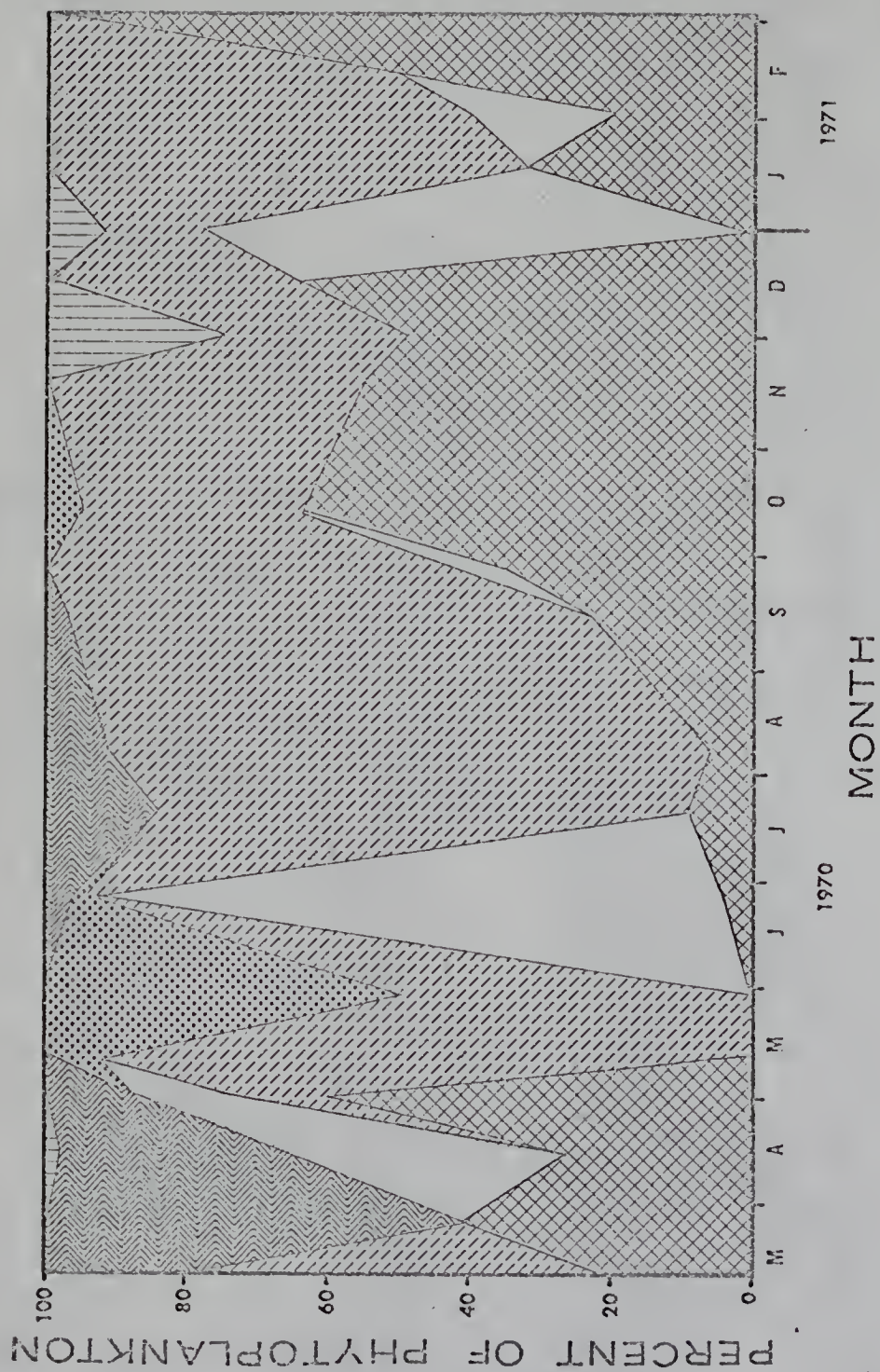


TABLE 4

Relationship between number of algal units and primary productivity

Lake-depth	r	95% bounds on ρ
Biven's Arm - surf.	0.12	$-.291 \leq \rho \leq .493$
McCloud - surf.	0.11	$-.345 \leq \rho \leq .523$
McCloud - 1.5 m	0.13	$-.635 \leq \rho \leq .766$

Figure 10. Variations in phytoplankton diversity for unfiltered samples from surface waters in Lake McCloud and Biven's Arm, 1970-1971.

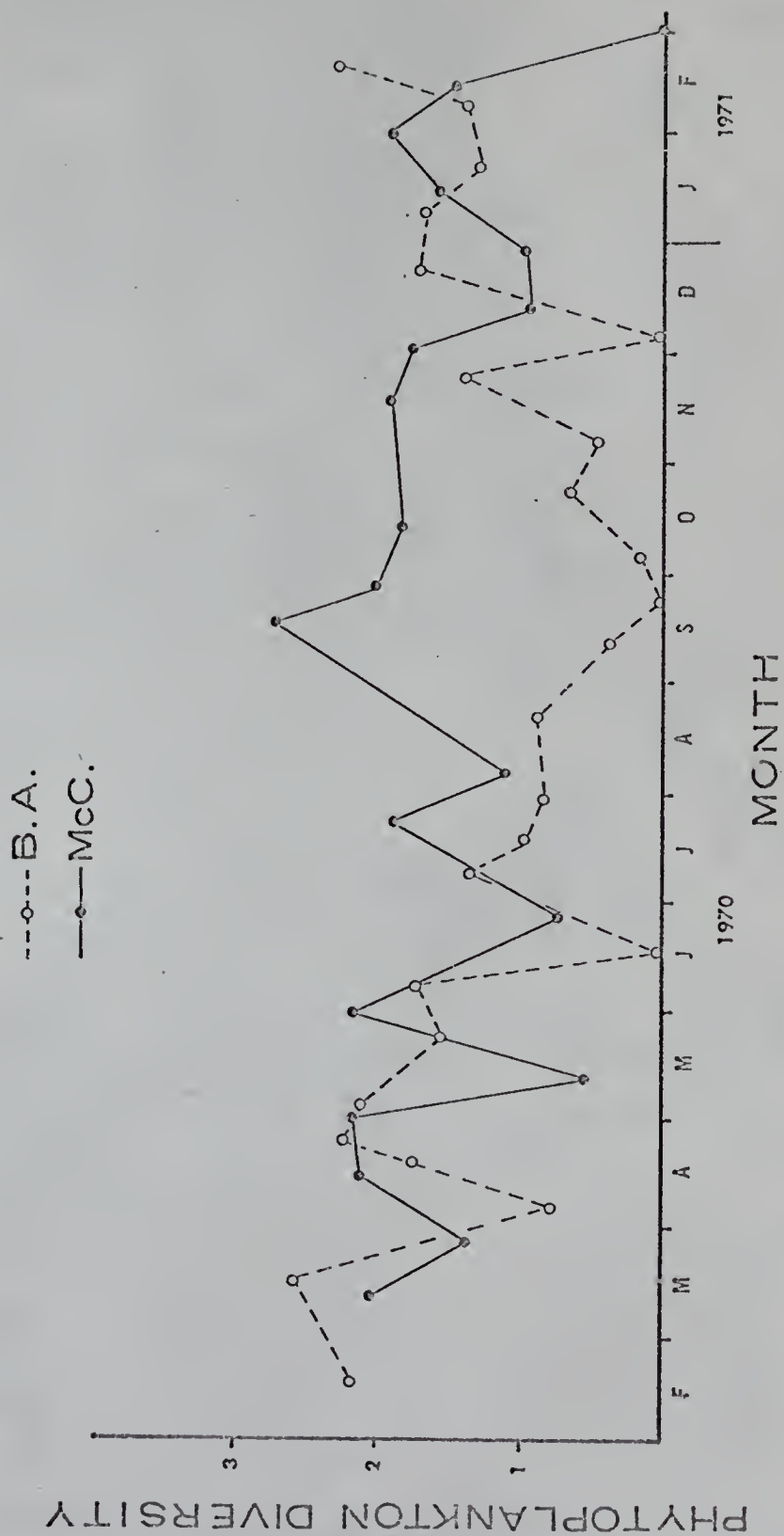


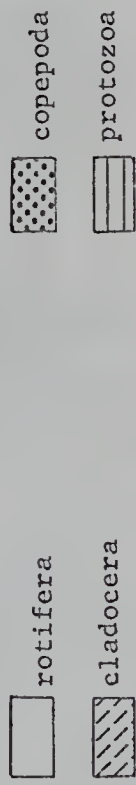
TABLE 5

Relationship between algal diversity and primary productivity

Lake-depth	r	95% bounds on ρ
Biven's Arm - surf.	0.24	$-.159 \leq \rho \leq .578$
McCloud - surf.	0.20	$-.264 \leq \rho \leq .592$
McCloud - 1.5 m	0.55	$-.254 \leq \rho \leq .905$

Figure 11. Seasonal fluctuations in zooplankton in Biven's Arm, 1970-1971.
 (Depth of pattern represents the percent of total zooplankton
 comprised by each group. Read in the same manner as Figure 8.).

Key:



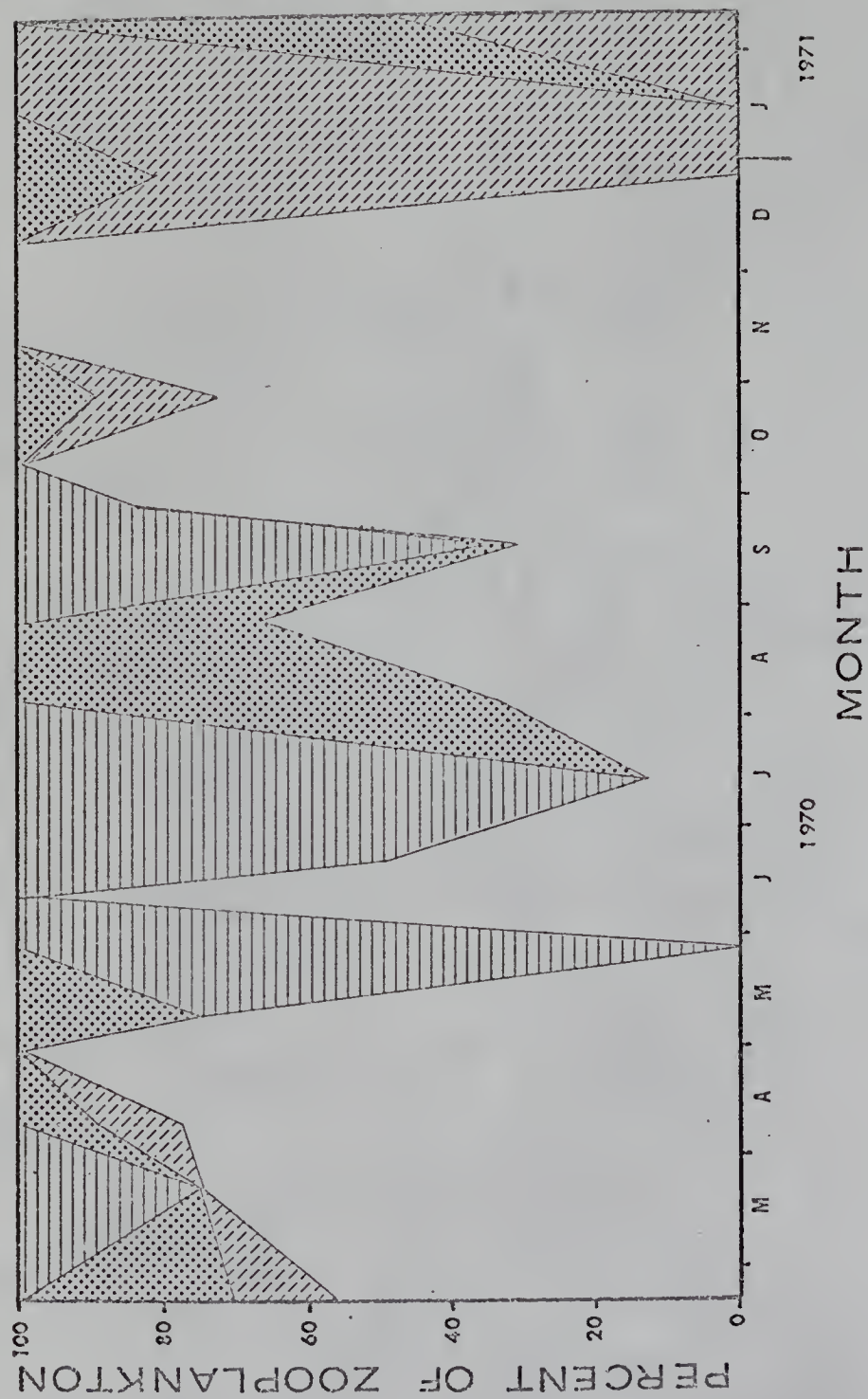
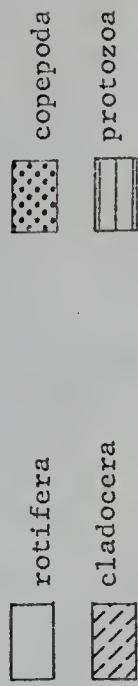


Figure 12. Seasonal fluctuations in zooplankton in Lake McCloud, 1970-1971.
 (Depth of pattern represents the percent of total zooplankton
 comprised by each group. Read in the same manner as Figure 8.)

Key:



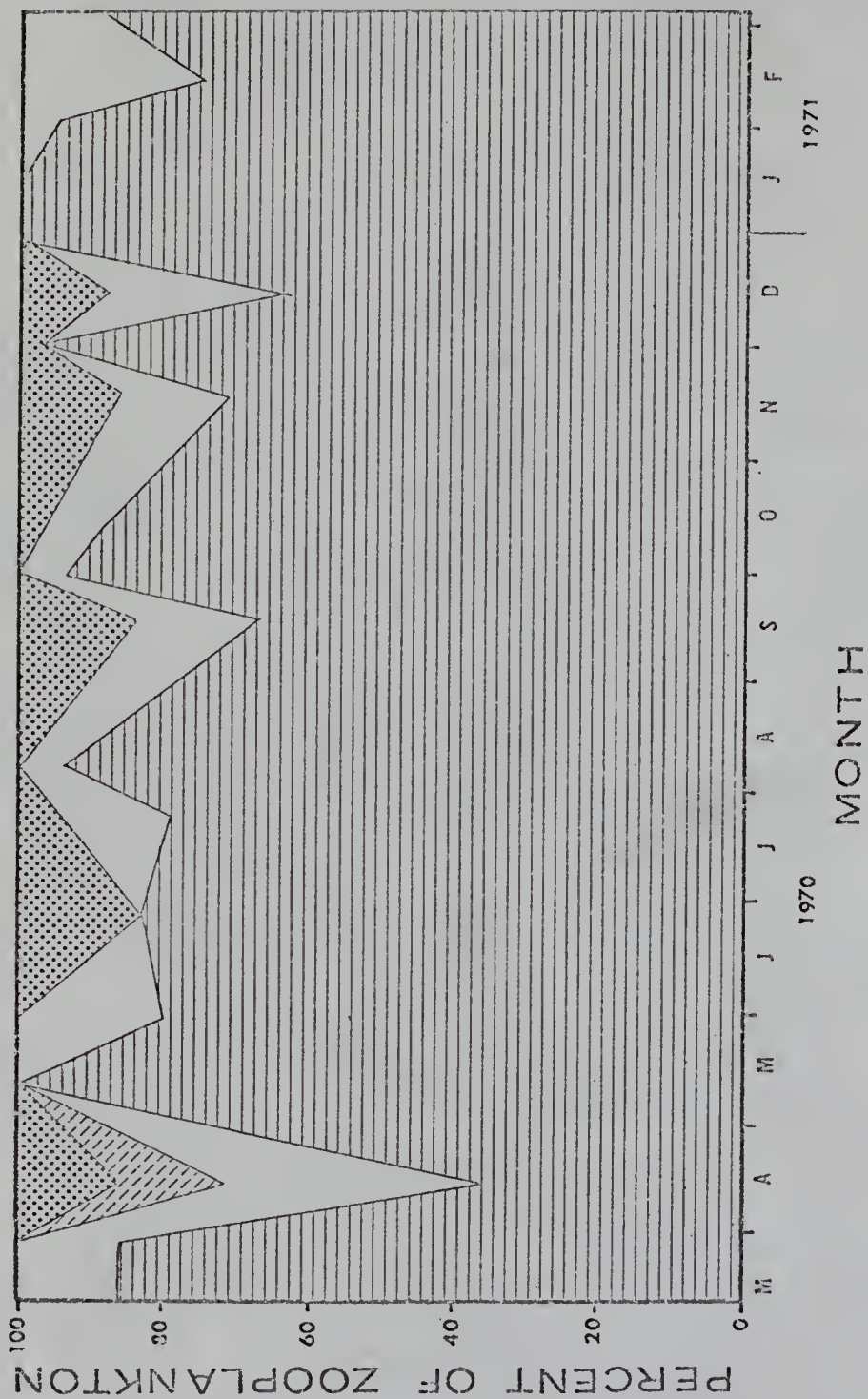


TABLE 6

Relationship between algal diversity and zooplankton numbers

Lake-depth	r	95% bounds on ρ
Biven's Arm - surf.	0.01	$-.454 \leq \rho \leq .470$
McCloud - surf.	0.25	$-.216 \leq \rho \leq .438$
McCloud - 1.5 m	0.66	$-.080 \leq \rho \leq .932$

DISCUSSION

Lake McCloud

The spring primary productivity pulse in Lake McCloud coincided with the appearance of diatoms (Figures 1, 2, and 9) and an increase in productivity by nannoplankton (Figure 4). However, total algal biomass, as indicated by numbers (Tables A1 - A10) and by chlorophyll (Figures 6 and 7) appeared to remain at a low level. Peaks in productivity in Lake McCloud might therefore be attributed to an increase in the efficiency of nutrient utilization reflected by the increase in nannoplankton productivity (Findenegg, 1965, Olive et al., 1968). Low numbers of nannoplankton during the primary productivity peaks (Table A4) and the relatively stable numbers of nannoplankton throughout the year reflect the efficiency of these small cells in productivity.

The fall pulse also corresponded with the appearance of diatoms but there was no corresponding increase in the productivity of nannoplankton. The gradual increase in the summer population of dinoflagellates seems to be more closely related to this autumn productivity pulse.

Dinobryon species are often found following nutrient depletion following an algal bloom (Lund, 1965, Hutchinson, 1967). The decrease in primary productivity and the parallel increase of Dinobryon sertularia after the spring and fall pulses could be attributed to a decrease in essential nutrients, specifically phosphates (Guseva, 1947, as reported by Lund, 1965).

The decrease in the magnitude of the bimodal pattern at 1.5 m might be attributed to lower light penetration at that level, not species composition, since species were similar in number and kind at both depths. Since the samples from 1.5 m were incubated at the same light intensities as the surface samples, some form of light inhibition could be postulated. Stratification is rare and never persistent in Lake McCloud, so the algae could become shade-adapted only on a short-term basis. Such major physiological adaptations as enzyme shifts which were proposed by Yentsch and Lee (1966) probably are not responsible for the lowered productivity.

The importance of nanoplankton in the productivity of Lake McCloud, as shown in Figure 5, fits the pattern predicted by Goldman and Wetzel (1963) in that nanoplankton appeared to be most important in winter and spring at the surface, and throughout the year at 1.5 m. The increase of nanoplankters at the time of the spring bloom has been attributed to their efficiency in the utilization of nutrients and to the inability of the larger species to capitalize as quickly on the nutrient pool due to their slower reproductive rates, growth rates and germination time from overwintering stages (Lund, 1965). The lack of nanoplankton dominance in the fall pulse indicates that resources were tied up in the biomass of the larger algae. Once the larger species died, the stored nutrients would be released, and the nanoplankton could increase in winter. The nanoplankton species appear to be able to utilize organic nutrients and to be tolerant of low light conditions (Rodhe, 1962), which permits reproductive success in winter and in deep waters.

As expected from studies of other lakes by Pieczynska and Szczepanska (1966), chlorophyll "a" concentration was a good indicator of primary productivity in Lake McCloud (Table 3). The lack of correlation at 1.5 m may be due to the small sample size ($n = 8$). An increase in the numbers of samples analyzed would probably show that chlorophyll "a" concentration correlated with the level of primary productivity throughout the lake, at all depths. Chlorophyll is a better indicator of productivity than numbers (Table 4) since numbers can include dead individuals, individuals with lowered or raised activity, or individuals of varying sizes and shapes. Fogg (1965) suggests that surface area is a more accurate indicator of productivity than numbers as it reflects biomass more accurately.

The species present in Lake McCloud, as indicated by chlorophyll content and microscopic investigation, were predominantly diatoms and dinoflagellates. Species such as Peridinium sp., Sphaerocystis sp. and Dinobryon sp. are indicative of low nutrient conditions (Hutchinson, 1967) while desmids such as Staurostrum spp. (Brook, 1965) are indicative of both low nutrient conditions and acid waters. Colonies of Dinobryon, as mentioned previously, are especially numerous in lakes recently depleted of nutrients by algal blooms.

The pattern of succession followed that described by Gliwicz (1967) and Margalef (1958). According to Gliwicz and Margalef, a spring bloom of algae that are rapid reproducers and efficient producers (such as diatoms, nanoplankton) is followed by an increase in importance of larger, more sluggish species that are more tolerant of low nutrient conditions (such as Dinobryon sp.). These species, being long-lived, slow nutrient turnover, leading to lowered productivity. In the fall, die-off of these larger species releases

stored nutrients to the water, allowing an autumn bloom, followed by another pulse of species tolerant of low nutrient conditions. The winter population of efficient, low-light tolerant species (such as nanoplankton) forms the "seed" population for the coming spring bloom.

In Lake McCloud, algal diversity was not indicative of primary productivity. Productivity appeared to be more closely related to the actual assemblage of species present rather than to the number of algae, the total biomass or the numbers of species present. Margalef (1965) proposed that algal diversity was directly correlated with primary productivity but this was not the case in Lake McCloud.

Zooplankton species (Figure 12) did not appear to change seasonally but those animals found in my samples were fewer and less diverse than those found in the same lake by other researchers (Maslin, 1969, Maslin, 1970). This was due to my failure to adjust collecting techniques for zooplankton, the more agile species being able to avoid the narrow mouth of the collecting devices. A subsequent underestimation of certain groups resulted. Maslin (1969) showed that some groups, notably copepods, appeared to be correlated with changes in productivity, and the peaks in zooplankton number that he found closely follow the increases in nanoplankton productivity found in this study. The nanoplankton are thought to be a principal source of food for herbivorous zooplankton (Nauwerk, 1963, as reported by Lund, 1967, Gliwicz, 1969a, 1969b, 1969c).

✓ In summary, Lake McCloud, defined as an acid, nutrient-poor lake, can be described using primary productivity, algal species and succession. In such a lake, algal species and size groups typical of the nanoplankton dominate primary productivity.

Biven's Arm

The seasonal periodicity in Biven's Arm did not completely resemble that in Lake McCloud (Figures 1, 2). A persistent summer bloom of blue-green algae, shown in Figure 8, coincided with a summer increase in primary productivity. Such blue-green algal blooms are not uncommon in shallow, wind-mixed lakes where nutrients can be kept in circulation throughout the year (Lund, 1965, 1967, Whitford and Schumacher, 1968). This apparently was the case in Biven's Arm.

Spring and fall pulses in productivity appeared to coincide with the appearance of the diatom, Melosira granulata. The spring bloom was also dominated by nanoplankton productivity (Figure 4) although no such dominance was apparent in the fall. This pattern is similar to that described for Lake McCloud, although the actual magnitude of productivity and the numbers of algae in Biven's Arm were generally greater than in Lake McCloud (Figures 1 - 4, Tables A1 - A6).

The tendency for productivity at 0.3 m to be greater than productivity at the surface (Table 2) was not due to an increase in numbers in the deeper waters (Tables A1, A7). Since 0.3 m is very near the bottom of Biven's Arm, it is possible that the increased productivity is due to the proximity of the algae to the nutrient-laden bottom sediments. In addition, fewer numbers of algae permit a reduction in competition between cells for available nutrients, even though light penetration is limited.

An increase in nanoplankton numbers in the spring bloom might be expected if an increase in nutrient content in the water accompanied a spring warming trend. Nordlie (1967) indicated that both nitrate and phosphate concentrations increased in May, following a slight

decrease in March and April, and coincided with a temperature rise beginning in March. Such a rise in available nutrients would allow the more efficient nanoplankton to reproduce rapidly until nutrients were exhausted and until the summer species began to appear.

During the remainder of the year, nanoplankton contributions were equal to or less than those of the nanoplankton in the summer in Lake McCloud. From this pattern, it appears that nanoplankton are not as important in the productivity of a eutrophic lake, except during a period of rapid increase in numbers such as in the spring bloom.

Neither chlorophyll "a" nor total chlorophyll content showed any significant relationship with primary productivity (Table 3). Pieczynska and Szczepanska (1966), and Winner (1969) indicated that the use of chlorophyll as an indicator of total viable biomass or of primary productivity became limited when chlorophyll concentrations increased above a certain level. Much of the chlorophyll then measured would be from green but inactive cells and detritus, and more chlorophyll would be found in cells operating below maximum efficiency due to shading or self-inhibition. Chlorophyll levels in Biven's Arm were rarely below 40 mg/ml, far above the level of 800 μ g/ml set by Pieczynska and Szczepanska. Similarly, in Lake McCloud, the chlorophyll level usually fell within the range of zero to one mg/ml and a positive correlation between primary productivity and chlorophyll "a" was noted in Lake McCloud.

Species present in Biven's Arm, as indicated by chlorophyll concentrations and microscopic examination, were predominantly diatoms and blue-green algae. Species such as Melosira sp., Pediastrum spp., Scenedesmus spp., Anabaena sp. and Microcystis sp.

are typical of eutrophic systems (Brook, 1965, Whitford and Schumacher, 1968, Hutchinson, 1967, Holland, 1968). Many species of blue-green algae, such as Anabaena and Microcystis, are also tolerant of high temperature ranges and bright light conditions. This results in blooms in heated surface waters in the summer when other algae are inhibited by light and temperature (Lund, 1969). In addition, several species of blue-green algae are capable of nitrogen fixation, notably Anabaena sp. (Lund, 1965). Blooms of Anabaena such as in June and July in Biven's Arm could then occur in nutrient-depleted waters when not even other blue-green algae could survive. Such blooms would also add to the nitrate "pool" in the system, permitting a rapid regrowth of formerly limited species. The frequent reappearance of the diatom, Melosira granulata, during the summer may be due to changes in the turbulence of the water. This species, although still viable, may sink to the bottom of the lake where it survives. Increased circulation in the water due to winds lifts portions of the bottom of the lake into the water column, and such reappearance does not necessarily indicate a change in nutrient status of the system (Lund, 1969).

The pattern of succession in Biven's Arm - an association of desmids, diatoms and colonial green algae followed by blue-green algae - also fits the pattern described by Margalef (1958) and Gliwicz (1967), and that found in Lake McCloud. With the exception of the summer bloom that resulted from wind-mixing that did not occur at deeper Lake McCloud, identical cycles of succession were followed.

The algal diversity of Biven's Arm decreased in summer during the bloom of blue-green algae (Figure 9). Often these blooms were

monospecific, or nearly so. It has been theorized (Hartman, 1960, as reported in Lund, 1965) that blue-green algae exude growth-inhibiting substances toxic to other species, and that these substances are most effective when the population is nearly a monoculture. Under such conditions, reproduction and growth of new species are curtailed until a die-off of the blue-green algae occurs. As a result, inefficient producers such as blue-green algae can maintain high population levels and a relatively high productivity level on the basis of sheer numbers. Because of this summer phenomenon, algal diversity did not correlate with primary productivity (Table 5). In fact, even higher productivity might be obtained from such monospecific cultures if total numbers of individuals were reduced. A higher productivity during the summer bloom occurred in the nanoplankton sample of Biven's Arm than in the unfiltered sample (Figures 1, 2). However, the species associations were the same. Filtration resulted in a reduction of numbers only, allowing more light penetration per cell, and more nutrients per cell. In such a situation, the blue-green algae exhibited an ability for increased productivity that is presumably held down by intraspecific competition in nature.

The zooplankton samples from Biven's Arm suffered from the same underestimation as those from Lake McCloud. However, a marked seasonality was apparent (Figure 11). Decreases in the importance of the rotifer population during an Anabaena bloom in June, 1970, and an absence of cladocera throughout the summer bloom of blue-green algae species were observed. This decrease in some zooplankton groups may be due to a lack of tolerance to warmer waters, higher light intensities or the algae themselves. Numbers of zooplankton did

not correlate with algal diversity (Table 6) since some species of small rotifers increased in numbers during the summer months. These species may have been feeding on bacteria associated with the sheath of Microcystis aeruginosa (Lund, 1967), a food source not accounted for in the algal counts.

In summary, Biven's Arm exhibits many of the patterns shown by Lake McCloud with respect to primary productivity patterns and nutrient cycling. These patterns are superimposed on patterns of productivity, algal succession and species composition common in eutrophic systems where "net" plankton assume the dominant role in productivity.

SUMMARY

In this study, the relationships between phytoplankton community structure and primary productivity in two Florida lakes of different trophic status were examined. The most important conclusions were:

1. Nannoplankton (algal species with a diameter less than 70 μ) dominated productivity in surface waters in winter and spring in oligotrophic Lake McCloud. Nannoplankton also contributed the major portion of primary productivity throughout the year at 1.5 m. In the eutrophic lake, Biven's Arm, nannoplankton were of major importance in the spring bloom only.

2. Spring and fall primary productivity pulses coincided with the appearance of diatoms in both lakes.

3. Spring and fall blooms were followed by species capable of reproductive success in nutrient-depleted waters in both lakes. In Lake McCloud, this species was Dinobryon sertularia, a species tolerant of low phosphate concentrations, while in Biven's Arm, Anabaena sp., a nitrogen-fixing blue-green alga, followed the pulse.

4. In Biven's Arm, a summer primary productivity pulse coincided with a bloom of blue-green algae.

5. Chlorophyll "a" concentrations were positively correlated with primary productivity in the surface waters of Lake McCloud only. Chlorophyll concentrations in Biven's Arm were too high to be useful as an indicator of productivity.

6. No correlation was found between primary productivity and algal diversity or algal numbers.

7. Increases in nanoplankton productivity were followed by increases in numbers of zooplankton, and by the reappearance of certain zooplankton species. Zooplankton species and numbers decreased during blooms of blue-green algae.

APPENDIX

TABLE A1

Primary productivity ($\text{mg C/m}^3 \text{ hr}$), chlorophyll (mg/ml) and algal unit count ($\#/\text{ml}$) data for unfiltered samples from surface waters in Lake McCloud and Biven's Arm.

Date	Lake McCloud			Biven's Arm		
	$\text{mgC/m}^3 \text{ hr}$	mg chlor/ml	$\# \text{ units/ml}$	mg chlor/ml	$\# \text{ units/ml}$	$\# \text{ units/ml}$
14/II/70	-----	-----	-----	-----	-----	5600
12/III/70	6.65	-----	45	-----	-----	-----
17/III/70	-----	-----	-----	-----	-----	7800
26/III/70	2.7	-----	104	-----	-----	-----
4/IV/70	-----	-----	-----	-----	-----	3400
13/IV/70	1.37	-----	103	-----	-----	-----
17/IV/70	-----	-----	-----	-----	-----	1000
23/IV/70	-----	-----	-----	-----	-----	5800
30/IV/70	0.03	-----	385	-----	-----	-----
4/V/70	-----	-----	-----	-----	-----	1400
11/V/70	3.05	-----	107	-----	-----	-----
22/V/70	-----	-----	-----	49.95	-----	4100
29/V/70	12.77	6.01	40	-----	-----	-----

TABLE A1 Continued

Date	mgC/m ³ hr	Lake McCloud mg chlor/ml	# units/ml	mgC/m ³ hr	Biven's Arm mg chlor/ml	# units/ml
6/VI/70	-----	-----	-----	9.50	65.43	5800
16/VI/70	-----	-----	-----	1.40	179.93	2500
26/VI/70	0.00	6.50	771	-----	-----	-----
8/VII/70	-----	-----	-----	3.35	108.73	1100
17/VII/70	-----	-----	-----	14.48	135.06	2700
21/VII/70	0.43	2.32	209	-----	-----	-----
29/VII/70	-----	-----	-----	14.99	132.80	2100
6/VIII/70	1.32	3.18	179	-----	-----	-----
21/VIII/70	-----	-----	-----	13.47	112.37	6200
11/IX/70	-----	-----	-----	12.85	121.71	2800
15/IX/70	4.11	13.43	105	-----	-----	-----
24/IX/70	-----	-----	-----	6.49	152.31	5700
28/IX/70	1.71	7.01	159	-----	-----	-----
5/X/70	-----	-----	-----	1.68	70.05	3400
12/X/70	25.35	8.20	178	-----	-----	-----

TABLE A1 Continued

Date	mgC/m ³ hr	Lake McCloud mg chlor/ml	# units/ml	mgC/m ³ hr	Biven's Arm mg chlor/ml	# units/ml
23/X/70	-----	-----	-----	3.24	98.51	5000
7/XI/70	-----	-----	-----	7.01	111.39	4100
17/XI/70	1.76	2.01	64	-----	-----	-----
24/XI/70	-----	-----	-----	4.09	70.52	1500
1/XII/70	0.19	5.01	69	-----	-----	-----
6/XII/70	-----	-----	-----	1.37	66.94	3500
15/XII/70	0.32	4.13	26	-----	-----	-----
23/XII/70	-----	-----	-----	2.98	61.38	3700
29/XII/70	0.26	7.77	193	-----	-----	-----
9/I/71	-----	-----	-----	5.42	109.77	4000
15/I/71	0.06	7.78	27	-----	-----	-----
22/I/71	-----	-----	-----	3.32	63.23	2600
31/I/71	0.22	0.00	44	-----	-----	-----
5/II/71	-----	-----	-----	4.69	29.46	5700
12/II/71	0.06	0.47	52	-----	-----	-----

TABLE A1 Continued

Date	mgC/m ³ hr	Lake McCloud mg chlor/ml	# units/ml	mgC/m ³ hr	Biven's Arm mg chlor/ml	# units/ml
19/II/71	-----	-----	-----	3.58	57.56	1600
1/III/71	3.65	11.28	9	-----	-----	-----

TABLE A2

Primary productivity ($\text{mgC}/\text{m}^3 \text{ hr}$), chlorophyll (mg/ml) and algal unit count ($\#/\text{ml}$) data for samples less than 158μ from surface waters in Lake McCloud and Biven's Arm.

Date	$\text{mgC}/\text{m}^3 \text{ hr}$	Lake McCloud $\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$	$\text{mgC}/\text{m}^3 \text{ hr}$	Biven's Arm $\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$
14/II/70	-----	-----	-----	6.84	-----	5700
12/III/70	2.31	-----	45	-----	-----	-----
17/III/70	-----	-----	-----	6.52	-----	7800
26/III/70	2.40	-----	44	-----	-----	-----
4/IV/70	-----	-----	-----	0.86	-----	1900
13/IV/70	1.05	-----	2	-----	-----	-----
17/IV/70	-----	-----	-----	1.80	-----	1700
23/IV/70	-----	-----	-----	0.89	-----	1700
30/IV/70	0.68	-----	72	-----	-----	-----
4/V/70	-----	-----	-----	1.01	-----	2100
11/V/70	4.69	-----	43	-----	-----	-----
22/V/70	-----	-----	-----	10.44	52.00	2700
29/V/70	10.73	14.86	76	-----	-----	-----
6/VI/70	-----	-----	-----	9.28	61.17	5200

TABLE A2 Continued

Date	mgC/m ³ hr	Lake McCloud mg chlor/ml	# units/ml	mgC/m ³ hr	Biven's Arm mg chlor/ml	# units/ml
16/VI/70	-----	-----	-----	9.89	146.13	2900
26/VI/70	0.85	4.14	62	-----	-----	-----
8/VII/70	-----	-----	-----	3.01	118.62	1000
17/VII/70	-----	-----	-----	13.57	123.24	2700
21/VII/70	0.67	4.58	116	-----	-----	-----
29/VII/70	-----	-----	-----	16.98	121.20	1900
6/VIII/70	1.17	1.82	162	-----	-----	-----
21/VIII/70	-----	-----	-----	12.60	122.58	3000
11/IX/70	-----	-----	-----	13.47	121.77	5600
15/IX/70	2.74	4.66	134	-----	-----	-----
24/IX/70	-----	-----	-----	6.08	166.32	5700
28/IX/70	1.68	4.27	223	-----	-----	-----
5/X/70	-----	-----	-----	1.74	66.38	5700
12/X/70	16.94	1.95	56	-----	-----	-----
23/X/70	-----	-----	-----	9.62	88.95	6700

TABLE A2 Continued

Date	mgC/m ³ hr	Lake McCloud mg chlor/ml	# units/ml	mgC/m ³ hr	Biven's Arm mg chlor/ml	# units/ml
7/XI/70	-----	-----	-----	5.21	85.68	7500
17/XI/70	1.18	4.30	107	-----	-----	-----
24/XI/70	-----	-----	-----	3.54	56.16	2000
1/XII/70	0.17	1.73	27	-----	-----	-----
6/XII/70	-----	-----	-----	0.71	51.26	100
15/XII/70	0.19	2.27	121	-----	-----	-----
23/XII/70	-----	-----	-----	3.65	60.47	6800
29/XII/70	0.18	1.45	27	-----	-----	-----
9/I/71	-----	-----	-----	5.67	88.60	2900
15/I/71	0.11	3.25	35	-----	-----	-----
22/I/71	-----	-----	-----	2.24	43.11	1700
31/I/71	0.14	0.96	18	-----	-----	-----
5/II/71	-----	-----	-----	4.71	20.33	2900
12/II/71	1.53	0.67	27	-----	-----	-----
19/II/71	-----	-----	-----	2.37	40.61	2300
1/III/71	2.71	0.29	18	-----	-----	-----

TABLE A3

Primary productivity ($\text{mgC}/\text{m}^3 \text{ hr}$), chlorophyll (mg/ml) and algal unit count ($\#/\text{ml}$) data for algae less than 76μ from surface waters in Lake McCloud and Biven's Arm.

Date	$\text{mgC}/\text{m}^3 \text{ hr}$	Lake McCloud $\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$	$\text{mgC}/\text{m}^3 \text{ hr}$	Biven's Arm $\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$
14/II/70	-----	-----	-----	4.81	-----	6200
12/III/70	1.64	-----	105	-----	-----	-----
17/III/70	-----	-----	-----	9.59	-----	4600
26/III/70	0.60	-----	26	-----	-----	-----
4/IV/70	-----	-----	-----	1.32	-----	900
13/IV/70	0.41	-----	9	-----	-----	-----
17/IV/70	-----	-----	-----	4.91	-----	1700
23/IV/70	-----	-----	-----	1.03	-----	2300
30/IV/70	0.52	-----	77	-----	-----	-----
4/V/70	-----	-----	-----	2.21	-----	4300
11/V/70	5.56	-----	36	-----	-----	-----
22/V/70	-----	-----	-----	9.60	58.39	2500
29/V/70	11.41	8.43	0	-----	-----	-----
6/VI/70	-----	-----	-----	10.01	52.61	4800

TABLE A3 Continued

Date	mgC/m ³ hr	Lake McCloud mg chlor/ml	# units/ml	mgC/m ³ hr	Biven's Arm mg chlor/ml	# units/ml
16/VI/70	-----	-----	-----	5.60	146.13	1900
26/VI/70	0.04	3.18	185	-----	-----	-----
8/VII/70	-----	-----	-----	2.51	101.31	900
17/VII/70	-----	-----	-----	9.42	86.68	3000
21/VII/70	0.44	5.06	229	-----	-----	-----
29/VII/70	-----	-----	-----	15.11	60.27	1600
6/VIII/70	0.84	2.68	113	-----	-----	-----
21/VIII/70	-----	-----	-----	13.81	109.29	5100
11/IX/70	-----	-----	-----	12.59	95.58	4800
15/IX/70	3.02	1.48	69	-----	-----	-----
24/IX/70	-----	-----	-----	5.18	132.82	5000
28/IX/70	0.78	3.26	35	-----	-----	-----
5/X/70	-----	-----	-----	1.89	53.56	4100
12/X/70	4.59	6.17	114	-----	-----	-----
23/X/70	-----	-----	-----	5.67	68.58	1300
7/XI/70	-----	-----	-----	5.14	73.14	6000

TABLE A3 Continued

Date	mgC/m ³ hr	Lake McCloud mg chlor/ml	# units/ml	mgC/m ³ hr	Biven's Arm mg chlor/ml	# units/ml
17/XI/70	0.94	5.69	70	-----	-----	-----
24/XI/70	-----	-----	-----	3.07	44.96	3000
1/XII/70	0.14	3.29	18	-----	-----	-----
6/XII/70	-----	-----	-----	0.85	37.31	700
15/XII/70	0.26	4.43	18	-----	-----	-----
23/XII/70	-----	-----	-----	3.13	46.70	5200
29/XII/70	0.14	0.38	53	-----	-----	-----
9/I/71	-----	-----	-----	3.38	16.06	3000
15/I/71	0.03	3.34	0	-----	-----	-----
22/I/71	-----	-----	-----	1.85	43.55	2600
31/I/71	0.02	2.08	0	-----	-----	-----
5/II/71	-----	-----	-----	3.32	17.66	1600
12/II/71	1.98	0.38	9	-----	-----	-----
19/II/71	-----	-----	-----	2.65	47.64	2100
1/III/71	2.16	0.47	34	-----	-----	-----

TABLE A4

Primary productivity (mgC/m³ hr), chlorophyll (mg/ml) and algal unit count (#/ml) data for algae less than 70 μ from surface waters in Lake McCloud and Biven's Arm.

Date	mgC/m ³ hr	Lake McCloud mg chlor/ml	# units/ml	mgC/m ³ hr	Biven's Arm mg chlor/ml	# units/ml
14/II/70	-----	-----	-----	5.85	-----	4900
12/III/70	3.00	-----	35	-----	-----	-----
17/III/70	-----	-----	-----	0.00	-----	3400
26/III/70	1.00	-----	43	-----	-----	-----
4/IV/70	-----	-----	-----	1.01	-----	2100
13/IV/70	0.03	-----	0	-----	-----	-----
17/IV/70	-----	-----	-----	1.01	-----	2200
23/IV/70	-----	-----	-----	1.04	-----	1600
30/IV/70	0.68	-----	76	-----	-----	-----
4/V/70	-----	-----	-----	2.98	-----	2900
11/V/70	4.69	-----	26	-----	-----	-----
22/V/70	-----	-----	-----	10.37	60.99	1200
29/V/70	11.24	3.12	0	-----	-----	-----
6/VI/70	-----	-----	-----	7.63	54.61	4100

TABLE A4 Continued

Date	mgCm ³ hr	Lake McCloud mg chlor/ml	# units/ml	mgC/m ³ hr	Biven's Arm mg chlor/ml	# units/ml
16/VI/70	-----	-----	-----	5.13	179.93	1100
26/VI/70	0.36	5.62	61	-----	-----	-----
8/VII/70	-----	-----	-----	1.96	127.04	1100
17/VII/70	-----	-----	-----	6.97	51.40	1800
21/VII/70	0.26	21.15	34	-----	-----	-----
29/VII/70	-----	-----	-----	14.99	62.05	3400
6/VIII/70	0.59	5.76	117	-----	-----	-----
21/VIII/70	-----	-----	-----	14.50	98.44	4300
11/IX/70	-----	-----	-----	9.36	84.24	3100
15/IX/70	2.45	1.42	77	-----	-----	-----
24/IX/70	-----	-----	-----	3.96	112.25	5100
28/IX/70	0.54	4.19	36	-----	-----	-----
5/X/70	-----	-----	-----	3.03	62.12	3800
12/X/70	9.90	5.01	71	-----	-----	-----
23/X/70	-----	-----	-----	6.11	58.24	2800
7/XI/70	-----	-----	-----	5.19	66.17	4600

TABLE 4A Continued

Date	mgCm ³ hr	Lake McCloud mg chlor/ml	# units/ml	mgC/m ³ hr	Biven's Arm mg chlor/ml	# units/ml
17/XI/70	1.27	2.58	26	-----	-----	----
24/XI/70	-----	-----	-----	2.57	38.95	5400
1/XII/70	0.18	1.58	9	-----	-----	----
6/XII/70	-----	-----	-----	1.01	41.61	3200
15/XII/70	0.29	0.29	17	-----	-----	----
23/XII/70	-----	-----	-----	2.97	50.20	6300
29/XII/70	0.18	1.16	105	-----	-----	----
9/I/71	-----	-----	-----	2.47	31.73	4100
15/I/71	0.09	1.71	18	-----	-----	----
22/I/71	-----	-----	-----	1.44	31.51	2900
31/I/71	0.17	4.43	26	-----	-----	----
5/II/71	-----	-----	-----	1.76	17.49	1700
12/II/71	0.80	1.04	9	-----	-----	----
19/II/71	-----	-----	-----	1.78	46.55	1400
1/III/71	1.63	0.47	45	-----	-----	----

TABLE A5

Primary productivity ($\text{mgC}/\text{m}^3 \text{ hr}$) and chlorophyll11 (mg/ml) data for algae greater than 8μ from surface waters in Lake McCloud and Biven's Arm.

Date	Lake McCloud		Biven's Arm	
	$\text{mgC}/\text{m}^3 \text{ hr}$	$\text{mg chlor}/\text{ml}$	$\text{mgC}/\text{m}^3 \text{ hr}$	$\text{mg chlor}/\text{ml}$
8/VII/70	-----	-----	3.36	104.89
17/VII/70	-----	-----	13.74	137.16
21/VII/70	0.44	21.45	-----	-----
29/VII/70	-----	-----	14.90	137.40
6/VIII/70	1.21	3.24	-----	-----
21/VIII/70	-----	-----	14.24	115.54
11/IX/70	-----	-----	12.92	114.96
15/IX/70	4.40	21.51	-----	-----
24/IX/70	-----	-----	7.52	136.94
28/IX/70	2.06	6.07	-----	-----
5/X/70	-----	-----	2.05	68.18
12/X/70	22.50	3.07	-----	-----
23/X/70	-----	-----	10.69	100.83
7/XI/70	-----	-----	7.08	104.11

TABLE A5 Continued

Date	Lake McCloud		Biven's Arm	
	mgC/m ³	hr	mgC/m ³	hr
	mg chlor/ml		mg chlor/ml	
17/XI/70	1.92	3.45	-----	-----
24/XI/70	-----	-----	4.44	75.50
1/XII/70	0.20	4.93	-----	-----
6/XII/70	-----	-----	1.54	60.84
15/XII/70	0.32	8.48	-----	-----
23/XII/70	-----	-----	3.25	80.64
29/XII/70	0.27	0.47	-----	-----
9/I/71	-----	-----	6.90	141.63
15/I/71	0.07	2.41	-----	-----
22/I/71	-----	-----	2.89	69.16
31/I/71	0.21	6.71	-----	-----
5/II/71	-----	-----	6.22	30.03
12/II/71	0.08	0.77	-----	-----
19/II/71	-----	-----	3.59	54.60
1/III/71	3.51	1.01	-----	-----

TABLE A6

Primary productivity ($\text{mgC}/\text{m}^3 \text{ hr}$) and chlorophyll (mg/ml) data for algae greater than 5μ from surface waters in Lake McCloud and Biven's Arm.

Date	Lake McCloud		Biven's Arm	
	$\text{mgC}/\text{m}^3 \text{ hr}$	$\text{mg chlor}/\text{ml}$	$\text{mgC}/\text{m}^3 \text{ hr}$	$\text{mg chlor}/\text{ml}$
8/VII/70	-----	-----	3.04	109.96
17/VII/70	-----	-----	15.67	114.89
21/VII/70	0.39	19.08	-----	-----
29/VII/70	-----	-----	14.49	133.70
6/VIII/70	1.12	7.96	-----	-----
21/VIII/70	-----	-----	14.41	117.83
11/IX/70	-----	-----	12.76	110.14
15/IX/70	3.41	12.90	-----	-----
24/IX/70	-----	-----	7.84	151.37
28/IX/70	1.98	7.01	-----	-----
5/X/70	-----	-----	1.38	75.08
12/X/70	22.20	3.09	-----	-----
23/X/70	-----	-----	9.17	78.28
7/XI/70	-----	-----	7.28	100.95

TABLE A6 Continued

Date	Lake McCloud mgC/m ³ hr	mg chlor/ml	Biven's Arm mgC/m ³ hr	mg chlor/ml
17/XI/70	1.65	1.78	-----	-----
24/XI/70	-----	-----	4.52	72.51
1/XII/70	0.23	2.47	-----	-----
6/XII/70	-----	-----	1.66	64.41
15/XII/70	0.35	4.93	-----	-----
23/XII/70	-----	-----	3.20	89.65
29/XII/70	0.29	1.01	-----	-----
9/I/71	-----	-----	6.08	123.72
15/I/71	0.07	1.68	-----	-----
22/I/71	-----	-----	3.07	78.56
31/I/71	0.22	0.00	-----	-----
5/II/71	-----	-----	5.53	34.54
12/II/71	0.07	1.02	-----	-----
19/II/71	-----	-----	3.61	66.29
1/III/71	3.72	0.00	-----	-----

TABLE A7

Primary productivity ($\text{mgC}/\text{m}^3 \text{ hr}$), chlorophyll (mg/ml) and total algal unit count ($\#/\text{ml}$) data for unfiltered samples from deeper waters in Lake McCloud and Biven's Arm.

Date	$\text{mgC}/\text{m}^3 \text{ hr}$	Lake McCloud $\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$	$\text{mgC}/\text{m}^3 \text{ hr}$	Biven's Arm $\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$
12/III/70	1.95	-----	19	-----	-----	----
17/III/70	-----	-----	-----	3.4	-----	11800
11/V/70	3.66	-----	70	-----	-----	----
26/V/70	1.86	3.74	108	-----	-----	----
6/VIII/70	0.63	8.01	201	-----	-----	----
24/IX/70	-----	-----	-----	7.73	145.32	4500
28/IX/70	1.81	11.38	156	-----	-----	----
12/X/70	7.63	10.36	37	-----	-----	----
6/XII/70	-----	-----	-----	0.33	73.83	1400
15/XII/70	0.12	0.77	35	-----	-----	----
19/II/71	-----	-----	-----	4.19	65.54	3300
1/III/71	0.51	1.78	70	-----	-----	----

TABLE A8

Primary productivity ($\text{mgC}/\text{m}^3 \text{ hr}$), chlorophyll (mg/ml) and algal unit count ($\#/\text{ml}$) data for algae less than 158μ from deeper waters in Lake McCloud and Biven's Arm.

Date	$\text{mgC}/\text{m}^3 \text{ hr}$	Lake McCloud - 1.5 m $\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$	$\text{mgC}/\text{m}^3 \text{ hr}$	Biven's Arm - 0.3 m $\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$
12/III/70	1.20	-----	89	-----	-----	----
17/III/70	-----	-----	-----	5.03	-----	10500
11/V/70	6.80	-----	404	-----	-----	----
26/VI/70	0.08	4.97	61	-----	-----	----
6/VIII/70	1.06	2.03	150	-----	-----	----
24/IX/70	-----	-----	-----	7.25	154.31	6200
28/IX/70	1.32	10.20	146	-----	-----	----
12/X/70	6.38	3.63	105	-----	-----	----
6/XII/70	-----	-----	-----	0.68	61.35	1600
15/XII/70	0.12	0.86	43	-----	-----	----
19/II/71	-----	-----	-----	2.47	44.27	2100
1/III/71	0.18	0.95	52	-----	-----	----

TABLE A9

Primary productivity ($\text{mgC}/\text{m}^3 \text{ hr}$), chlorophyll (mg/ml) and algal unit count data ($\#/\text{ml}$) for algae less than 76μ from deeper waters in Lake McCloud and Biven's Arm.

Date	$\text{mgC}/\text{m}^3 \text{ hr}$	Lake McCloud - 1.5 m		Biven's Arm - 0.3 m	
		$\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$	$\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$
12/III/70	1.31	-----	35	-----	-----
17/III/70	-----	-----	-----	-----	5100
11/V/70	5.94	-----	26	-----	-----
26/VI/70	0.69	5.44	17	-----	-----
6/VIII/70	1.12	3.77	69	-----	-----
24/IX/70	-----	-----	-----	128.72	6200
28/IX/70	1.68	4.98	9	-----	-----
12/X/70	6.87	3.60	44	-----	-----
6/XII/70	-----	-----	-----	33.87	600
15/XII/70	0.10	2.12	18	-----	-----
19/II/71	-----	-----	-----	49.63	2100
1/III/71	0.004	2.97	17	-----	-----

TABLE A10

Primary productivity ($\text{mgC}/\text{m}^3 \text{ hr}$), chlorophyll (mg/ml) and algal unit count ($\#/\text{ml}$) data for algae less than 70μ from deeper waters in Lake McCloud and Biven's Arm.

Date	$\text{mgC}/\text{m}^3 \text{ hr}$	Lake McCloud - 1.5 m		Biven's Arm - 0.3 m	
		$\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$	$\text{mg chlor}/\text{ml}$	$\# \text{ units}/\text{ml}$
12/III/70	0.42	-----	17	-----	-----
17/III/70	-----	-----	-----	-----	4800
11/V/70	2.25	-----	52	-----	-----
26/VI/70	1.88	3.63	35	-----	-----
6/VIII/70	0.69	6.30	69	-----	-----
24/IX/70	-----	-----	-----	129.17	5800
28/IX/70	1.76	8.95	43	-----	-----
12/X/70	7.18	1.53	114	-----	-----
6/XII/70	-----	-----	-----	34.98	300
15/XII/70	0.15	0.75	9	-----	-----
19/II/71	-----	-----	-----	44.39	2400
1/III/71	0.12	0.66	17	-----	-----

TABLE A11

Zooplankton numbers (#/liter) for unfiltered samples,
surface waters, in Lake McCloud and Biven's Arm.

Date	Lake McCloud	Biven's Arm
14/II/70	-----	1.0×10^3
12/III/70	1.3×10^3	-----
17/III/70	-----	3.3×10^3
26/III/70	0.7×10^3	-----
4/IV/70	-----	1.7×10^3
13/IV/70	2.3×10^3	-----
17/IV/70	-----	0.0
23/IV/70	-----	1.0×10^3
30/IV/70	0.3×10^3	-----
4/V/70	-----	1.0×10^3
11/V/70	1.7×10^3	-----
22/V/70	-----	0.3×10^3
29/V/70	0.0	-----
6/VI/70	-----	0.3×10^3
16/VI/70	-----	29.0×10^3
26/VI/70	1.7×10^3	-----
8/VII/70	-----	5.0×10^3
17/VII/70	-----	0.0
21/VII/70	3.3×10^3	-----
29/VII/70	-----	0.3×10^3
6/VIII/70	2.7×10^3	-----
21/VIII/70	-----	1.3×10^3
11/IX/70	-----	8.0×10^3
15/IX/70	1.3×10^3	-----

TABLE A11 Continued

Date	Lake McCloud	Biven's Arm
24/IX/70	-----	3.3×10^3
28/IX/70	3.3×10^3	-----
5/X/70	-----	0.3×10^3
12/X/70	3.3×10^3	-----
23/X/70	-----	2.6×10^3
7/XI/70	-----	0.7×10^3
17/XI/70	2.0×10^3	-----
24/XI/70	-----	0.3×10^3
1/XII/70	1.0×10^3	-----
6/XII/70	-----	6.0×10^3
15/XII/70	1.0×10^3	-----
23/XII/70	-----	2.3×10^3
29/XII/70	1.3×10^3	-----
9/I/71	-----	0.7×10^3
15/I/71	1.3×10^3	-----
22/I/71	-----	0.0
31/I/71	3.0×10^3	-----
5/II/71	-----	1.3×10^3
12/II/71	1.0×10^3	-----
19/II/71	-----	0.0
1/III/71	1.7×10^3	-----

TABLE A12

List of phytoplankton species found in unfiltered samples,
surface waters, in Lake McCloud and in Biven's Arm.

Division*	Lake McCloud	Biven's Arm
Cyanophyta	<u>Agmenellum</u> sp.	<u>Microcystis aeruginosa</u>
		<u>Anabaena circinalis?</u>
Euglenophyta		unidentified flagellates
Chlorophyta	colonial green algae	<u>Sphaerocystis</u> sp
	filamentous green alga	<u>Coelastrum</u> sp
	<u>Pediastrum</u> sp.	<u>Pediastrum</u> spp (2) [#]
		<u>Ankistrodesmus</u> sp
	<u>Scenedesmus</u> sp.	<u>Scenedesmus</u> spp (2)
	<u>Closterium</u> sp	<u>Tetraëdon</u> sp.
	<u>Staurastrum</u> spp (5)	<u>Staurastrum</u> sp.
	<u>Staurastrum cornutum</u>	colonial green algae
Chrysophyta	<u>Mallomonas</u> sp.	<u>Botryococcus</u> sp.
	<u>Dinobryon sertularia</u>	
Pyrrophyta	<u>Ceratium</u> sp	
	unidentified dinoflagellates (2)	
Bacillariophyceae		<u>Melosira granulata</u>
	<u>Melosira</u> sp.	<u>Cyclotella</u> sp.
	<u>Cyclotella</u> sp.	unidentified diatoms
	<u>Asterionella formosa</u>	
	unidentified diatoms	

* Divisions according to Edmondson, 1966.

Figures in parentheses refer to the number of distinct species found in the genus.

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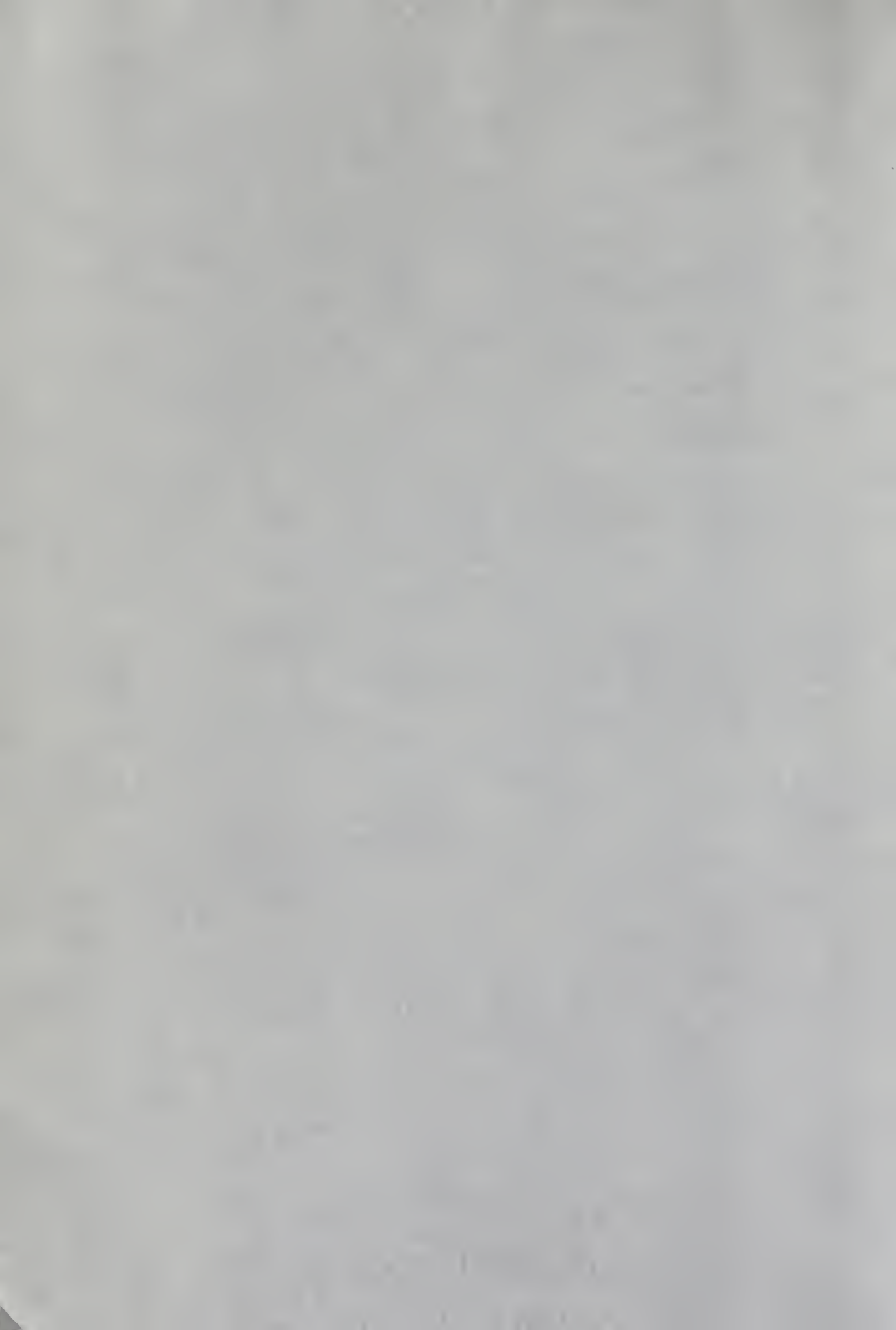
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



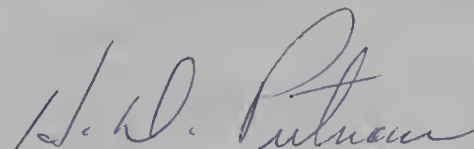
R. M. DeWitt, Chairman
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



F. G. Nordlie, Co-Chairman
Associate Professor of Zoology

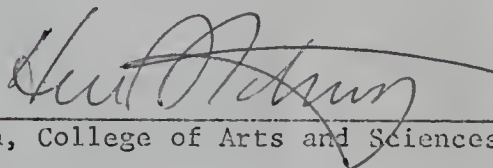
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



H. D. Putnam
Professor of Environmental Engineering

This dissertation was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1971



Dean, College of Arts and Sciences

Dean, Graduate School

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